PALAEOSCOLECID WORMS FROM THE MIDDLE CAMBRIAN OF AUSTRALIA

by KLAUS J. MÜLLER *and* INGELORE HINZ-SCHALLREUTER

ABSTRACT. The Middle Cambrian of the Georgina Basin, Queensland, Australia, has yielded a large association of secondarily phosphatized Palaeoscolecida in three-dimensional preservation. Many hitherto unknown details are described, such as the differentiated aboral end, irregularly distributed tubules on the outer surface, and a wide range of sclerites even on the same animal. Internal structure, functional morphology, ecological aspects and systematic relationships are also discussed. Nineteen species belonging to nine genera are described, of which the following are new: *Austroscolex primitivus* gen. et sp. nov., *A. spatiolatus* sp. nov., *Corallioscolex gravius* gen. et sp. nov., *Euryscolex paternarius* gen. et. sp. nov., *Kaloscolex granulatus* gen. et sp. nov., *Milaculum elongatum* sp. nov., *Murrayscolex inaequalis* gen. et sp. nov., *M. serratus* sp. nov., *Pantoioscolex oleschinskii* gen. et sp. nov., *Rhomboscolex chaoticus* gen. et sp. nov., *Schistoscolex angustosquamatus* gen. et sp. nov., *S. mucronatus* sp. nov., *S. umbilicatus* sp. nov., *Shergoldiscolex nodosus* gen. et sp. nov., *S. polygonatus* sp. nov., and *Thoracoscolex armatus* gen. et sp. nov.

PALAEOSCOLECIDA are a group of Early Palaeozoic worms that are characterized by annulation and a striking surface ornamentation. Minute plates of variable shape are arranged in rows perpendicular to the long axis over the armoured part of the organism. Such fossils have been known for more than 110 years (*Protoscolex* was described by Ulrich in 1878), but until recently received little attention. They are proving to be widespread in the early Phanerozoic, and may be of interest with regard to their possible stratigraphical applicability. As more-or-less entire fossils, they are preserved only under special conditions, mainly in shales. Much more widespread are the sclerotized plates from their surfaces. These are quite diverse, and have been described under different generic names, such as *Hadimopanella*, *Kaimenella*, and *Milaculum*. Such isolated plates have been recorded from all over the world; they range from the Early Cambrian to the Late Silurian.

The material presented herein is the most comprehensive association yet known. It is secondarily phosphatized and was etched from limestones. In this special type of preservation the specimens have survived in three dimensions, and for the first time the aboral end of the organisms can be documented. The end is usually broken. The worms are expected to have had a proboscis that underwent rapid decay because of its softer integument. Different types of sclerites may occur on the same animal, and variability in sclerite size and morphology can be studied in detail. Our material shows that generic assignment of isolated plates may be extremely difficult in some cases.

HISTORICAL REVIEW

In the study of Palaeoscolecida we have to distinguish between descriptions of more-or-less entire organisms embedded in shale and isolated sclerites. The source of the sclerites was discovered only recently (Hinz *et al.* 1990).

The first palaeoscolecidan worms were described by Ulrich (1878) under the generic name *Protoscolex*. This author introduced five species but the holotype of the type species (*P. covingtonenesis*), in particular, lacks distinctive features (Conway Morris *et al.* 1982, p. 2154). Therefore, the other four species of Ulrich (1878) and all subsequent assignments to this genus should be revised. Miller and Faber (1892) established *Protoscolex magnus* from the Upper

[Palaeontology, Vol. 36, Part 3, 1993, pp. 549–592.]

Ordovician Fulton Formation in Cincinnati, Ohio. They assigned the genus tentatively to the Annelida. Almost 30 years later, Bather (1920) described *Protoscolex latus* from the Lower Ludlow of Herefordshire. His drawing shows a double row of plates on each annulus. One row is smaller and sometimes overlain by the adjacent 'segment' so that the annulus appears to have only one row of plates. Details of spacing, outer shape and ornamentation of plates are not recorded. Bather considered the papillae as initial stages of setae (see below). On the basis of the cuticle, missing appendages and the presence of a gut, he stated a strong resemblance between *Protoscolex* and Oligochaeta, comparing the genus also with Nematoda and Millipedia. Further, he regarded the Upper Carboniferous *Pronaidites carbonarius* Kůsta, 1888 as *Protoscolex*, but this genus was included in the oligochaetid family Tubificidae Vejdovsky, 1884 by Howell (1962). Ruedemann (1925*a*) published *Protoscolex* cf. *covingtonensis* Ulrich from argillaceous black shales from a bed that is transitional between the Upper Ordovician Utica and Frankfort beds in upper New York State. Another, but questionable representative, *P. giganteus* Ruedemann, 1925*a*, is extremely large, being about 100 mm in length. The central canal of the specimen is apparently filled with mud. In the same year Ruedemann (1925*b*) described *Protoscolex batheri* from the Silurian Lockport Limestone at Gasport, New York and supported a relationship of *Protoscolex* to Oligochaeta.

Whittard (1953) introduced *Palaeoscolex* and the Palaeoscolecidae for worms that had a papillate surface but were more advanced than *Protoscolex*. The suggested separation between *Palaeoscolex* and *Protoscolex* was supported by Howell (1962) who maintained the Palaeoscolecidae but classified *Protoscolex* under phylum, class, order and family uncertain. The next palaeoscolecid was described by Robison (1969) as *Palaeoscolex ratcliffei* from the Middle Cambrian Spence Shale of Utah. The single, carbonized specimen is split longitudinally in the centre and therefore does not show the surface of the sclerites; Conway Morris and Robison (1986) published additional material from Spain, and established the new Class Palaeoscolecida. Due to the above-mentioned preservational differences, *P.* cf. *ratcliffei* could not properly be identified with Robison's (1969) species. The new material still left the problem of both ends, annulus borders, metameric segmentation and ornamentation of the individual plates unsolved. In connection with the description of a possible annelid from the Trenton Limestone (Ordovician) of Quebec, Conway Morris *et al.* (1982) discussed *Protoscolex* and *Palaeoscolex*, concluding that their interpretation as oligochaetes is not credible. They preferred a general assignment to the Annelida. Glaessner (1979) described *Palaeoscolex antiquus* from the Lower Cambrian Emu Bay silty shale or siltstone of Kangaroo Island, Australia. These fossils are preserved either as moulds or as partial replacements by calcite. They were rejected as palaeoscolecidan by some authors (e.g. Huo and Chen 1989). Xian and Huo (1988) recorded *Palaeoscolex sinensis* from South China.

A more comprehensive study was provided by Kraft and Mergl (1989) who described various new genera from the Lower Ordovician of Bohemia. Their well-preserved material came from clayey or micaceous shales and siliceous nodules. They tentatively assigned the fossils to the Annelida.

Isolated sclerites of Palaeoscolecida have been established under various generic names as hard parts of problematic affinity. Ethington and Clark (1965) were the first to report material discovered in the course of routine etching for conodonts from the Lower Ordovician of Alberta, Canada, and described the specimens as 'plate forms A and B' (non form C, which is enigmatic). Müller (1973) introduced *Milaculum* for four species, including Ethington and Clark's material, from Upper Cambrian and Ordovician strata of Iran, Sweden and North America. Müller and Miller (1976) described possible cysts as *Utahphospha* from limestones of the Upper Cambrian Orr Formation, Utah. Repetski (1981) followed with another species of these cysts from the Ordovician Padre Formation, Texas. He suggested that *Hadimopanella* and *Lenargyrion* might be junior synonyms of *Utahphospha* if they agreed in their internal structure. Further taxa were almost simultaneously published as *Hadimopanella* Gedik, 1977 (from the Upper Cambrian of Turkey) and *Lenargyrion* Bengtson, 1977 (from the Lower Cambrian of Siberia). Until now, *Lenargyrion* has been considered as a junior synonym of *Hadimopanella*. During the 1980s, many new, mostly hadimopanellid, species were described. Gedik (1981, 1989) established further taxa and proposed a hadimopanellid-based zonation for the entire Cambrian. Wrona (1982) and Gazdzicki and Wrona (1986) recognized

Hadimopanella apicata from the Lower Cambrian of Antarctica. Van den Boogaard (1983) reported hadimopanellids in rock-forming quantities from the Middle Cambrian Lancara Formation, northwestern Spain. Peel and Larsen (1984) described material from the Lower Cambrian of Greenland. Dzik (1986) erected a *Hadimopanella–Utahphospha* group. Wrona (1987) illustrated a fragment of a natural assemblage of hadimopanellid sclerites in quite an irregular and loose arrangement. He suggested a tube-like structure for the animal. Further, he established a family Utahphosphidae comprising *Utahphospha* and *Hadimopanella*, and considered *Milaculum* to be analogous but not homologous to Utahphosphidae. Märss (1988) introduced another palaeoscolecid under the name *Kaimenella* which is similar to *Milaculum*. Having been unaware of Wrona's (1987) paper he erected the Hadimopanellidae for *Hadimopanella* and *Kaimenella*. Boogaard (1988) described two new *Milaculum* species from the Upper Ordovician of Estonia and the Lower Silurian of the Welsh Borderland. He was the first to illustrate sclerites of different sizes in their original configuration, embedded in fragments of the preserved cuticle (Boogaard 1989*a*). In a second paper (Boogaard 1989*b*), he described another possible hadimopanellid species from the Ordovician of Estonia. Bendix-Almgreen and Peel (1988) agreed with a relationship between *Hadimopanella* and *Utahphospha*, but contrary to Repetski (1981), they kept them apart. In their study of material from the Lower Cambrian of North Greenland they were largely engaged in the question of internal structure and hadimopanellid affinity. Wang (1990) recorded a further *Hadimopanella* from the Silurian (Llandovery) Wangjiawan Formation of South China. Esakova (*in* Koneva *et al.* 1990) described a new species of *Utahphospha* from the Cambrian of Kazakhstan.

Contrary to the relatively intact worms which have been tentatively assigned to Annelida or even Oligochaeta, opinions about the nature of the sclerites have been quite diverse. Originally, they were described as problematica without any assignment. Bengtson (1977, p. 758) recognized *Lenargyrion* as external dermal sclerites, but pointed out that it '... shows no conclusive vertebrate characteristics. Any homologisation would be highly speculative and there remained a strong possibility of an unknown invertebrate origin that is unrelated to the vertebrate stock'. Wrona (1982, 1987) compared *Hadimopanella* with placoid scales of early vertebrates (heterostracans) but refrained from any systematic assignment. Dzik (1986) suggested that his *Hadimopanella–Utahphospha* group together with *Milaculum* Müller, 1973, could represent an evolutionary line of dermal skeleton in primitive chordates. Märss (1988) noted some similarity to Agnatha but did not commit herself with regard to the origin of the sclerites. Boogaard (1988, p. 8) considered the characteristics of *Milaculum* as being 'suggestive of an agnathan affinity'. Based on a written communication by M. Mergl (June 1989), he shared the opinion that *Hadimopanella* and *Milaculum* belong to Palaeoscolecida (Boogaard 1989*a*). In his 1989*b* paper Boogaard (p. 12) noted a resemblance between palaeoscolecidan sclerites and dermal plates of primitive chordates. He concluded that they were 'not ancestral to chordates but perhaps have derived from the same stock'. Bendix-Almgreen and Peel (1988) recognized morphological similarities between *Hadimopanella* and *Utahphospha* on the one hand and ascidian spicules of *Cystodites* Drasche, 1884 on the other. Despite compositional differences, they tentatively proposed a relationship between these forms. Wrona (1989) followed the suggestions of previous authors about a relationship of *Hadimopanella* and dermal sclerites of primitive chordates.

MATERIAL AND METHODS

In the Middle Cambrian of the Georgina Basin, Queensland, Australia, seventy-four samples from nine localities proved to be productive for palaeoscolecid worms (Table 1). The rocks are deeply weathered down to about 200 metres. A total of 150 kg was etched with 15 per cent acetic acid on screens with a mesh size of 150 and 250 microns in order to differentiate the various fractions from the beginning. Subsequently, the finest residues from the bottom of the buckets were washed on a 0·063 mm screen. Without further treatment these residues were sorted under a binocular microscope. The majority of the approximately 3500 sorted specimens were originally fragmented, which prevents statements about the real frequency of the individuals. Also the assignment of the specimens to particular taxa proved to be very difficult without SEM photographs because ornamentation of plates and platelets are mostly indistinguishable under a binocular microscope. Even

TABLE 1. Palaeoscolecid localities, sample numbers and species distributions. Unidentified palaeoscolecids came from: (1) About 1 km north of Mt Murray, E 139° 58′ 6″, S 21° 48′ 50,4″, Cme (sample no. 6958); (2) Rogers Ridge, Trig. P., E 139° 58′ 50,4″, S 21° 45′ 41,4″, Cme (sample nos 7262, 7263, 7275, 7280, 7282–4); (3) North of Rogers Ridge, E 139° 36,6′, S 21° 44′ 50,4″, Cmi (sample nos 7302–4, 7306–8, 7310, 7311, 7313, 7317, 7319, 7320); (4) About 1 km north of Mt Murray, E 139° 58′ 27,6″, S 21° 48′ 50,4″, Cme (sample nos 7321, 7322, 7324–6, 7328, 7331–45, 7347–50); (5) Phosphate Hill, excavation T15, E 139° 58′ 2″, S 21° 53′ 26″, Cme (sample nos 7351–9, 7362–7, 7371, 7374–6); (6) Phosphate Hill, excavation V9, E 139° 58′ 2″, S 21° 56′ 36″, Cme (sample nos 7377, 7383, 7390, 7393, 7394, 7400, 7401); (7) North of Rogers Ridge, E 139° 59,6′, S 21° 44′ 21″, Cmd (sample no. 7407); (8) North of Rogers Ridge, E 139° 59,6′, S 21° 44′ 19″, Cme (sample no. 7414); (9) Thorntonia, section 418, E 138° 53,8′, S 19° 7,4′, Cmc (sample no. 7464); (10) BMR Duchess 18, E 139° 59′ 16,4″, S 21° 45′, Cme (sample nos 7502, 7503).

Explanation of abbreviations: Cme, Monastery Creek Formation (late Templetonian); Cmi, Inca Shale (late Templetonian – ?early Floran; Cmc, Currant Bush Limestone (Undillan); Cmd, Devoncourt Limestone (Undillan). Ap, *Austroscolex primitivus*; As, *Austroscolex spatiolatus*; Cf, *Corallioscolex formosus*; Ep, *Euryscolex paternarius*; HoI, aff. *H. oezguli* form species I; HoII, aff. *H. oezguli* form species II; Kg, *Kaloscolex gravius*; Me, *Milaculum elongatum*; Mi, *Murrayscolex inaequalis*; Ms, *Murrayscolex serratus*; Po, *Pantoioscolex oleschinskii*; Rc, *Rhomboscolex chaoticus*; Sa, *Schistoscolex angustosquamatus*; Sm, *Schistoscolex mucronatus*; Su, *Schistoscolex umbilicatus*; Si, *Schistoscolex* sp. indet.; Sn, *Shergoldiscolex nodosus*; Sp, *Shergoldiscolex polygonatus*; Ta, *Thoracoscolex armatus*; Ha, cf. *Hadimopanella apicata*; Pi, Pal. gen. indet. sp. A.

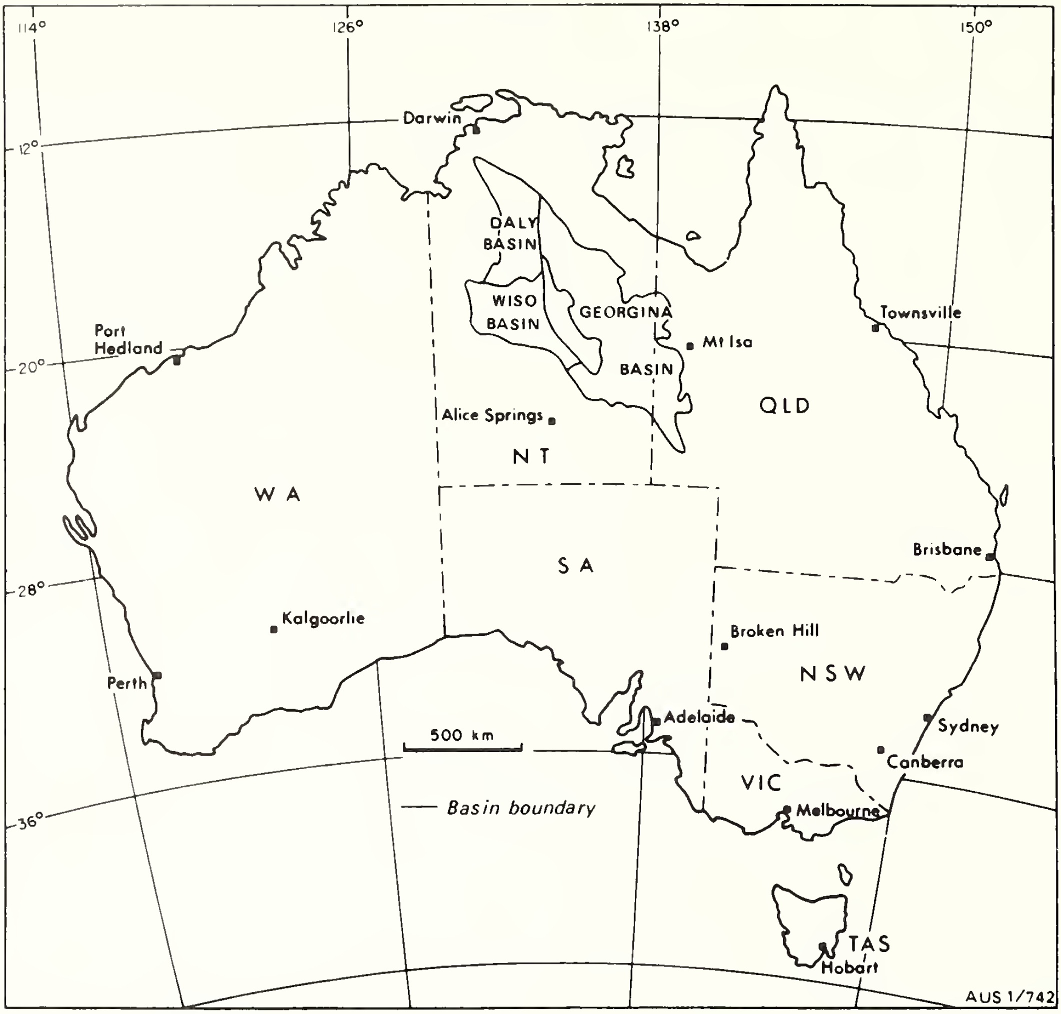
Locality	Age	Sample nos.	Ap	As	Cf	Ep	HoI	HoII	Kg	Me	Mi	Ms	Po	Rc	Sa	Sm	Su	Si	Sn	Sp	Ta	Ha	Pi
1 km N′ Mt Murray E 139° 58′ 27,6″; S 21° 48′ 50,4″	Cme	6958	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rogers Ridge, TP point E 139° 58′ 50,4″; S 21° 45′ 41,4″	Cme	7262	.	×	.	.	.	.	.	.	.	.	.	×	×	.	×	.	.	.	.	.	.
		7263	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	×
		7275	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7280	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7282	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7283	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	×
		7284	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
N′ Rogers Ridge E 139° 58′ 36,6″; S 21° 44′ 50,4″	Cmi	7302	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7303	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.
		7304	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7306	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

		7307	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7308	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7310	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.
		7311	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7313	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7317	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7319	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7320	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1 km N′ Mt Murray	Cme	7321	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
E 139° 58′ 27,6″;		7322	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S 21° 48′ 50,4″		7324	.	.	×	.	.	.	.	×	.	.	.	×	.	.	×	.	.	.	.	.	.
		7325	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7326	×	.	.	.	.	.	.	×	.	.	.	.	×	.	.	.	.	.	.	.	.
		7328	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7331	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.	.
		7332	.	.	.	.	.	.	.	.	.	.	.	.	×	×	.	.	.	.	.	.	.
		7333	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7334	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.	.
		7335	.	×	.	.	.	.	.	×	.	×	.	×	.	.	×	.	×	×	.	.	.
		7336	.	×	×	.	×	×	×	×	×	×	.	×	×	.	×	×	×	×	.	.	.
		7337	.	.	.	.	.	×	.	×	×	×	.	.	×	.	×	.	.	.	×	.	.
		7338	.	×	×	.	.	.	×	×	×	×	.	×	×	.	×	×	×	×	.	.	.
		7339	.	×	.	×	×	.	×	×	.	.	.	×	×	.	.	.	×	×	×	.	.
		7340	×	.	.	.	.	.	.	.	.	×	.	×	×	.	×	.	.	×	.	.	.
		7341	.	×	.	.	.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	.
		7342	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7343	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7344	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7345	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7347	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7348	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7349	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		7350	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE 1. Palaeoscolecid localities, sample numbers and species distributions. Unidentified palaeoscolecids came from (1) About 1 km north of Mt Murray, E 139° 58′ 6″, S 21° 48′ 50,4″, Cme (sample no 6958); (2) Rogers Ridge, Trig. P., E 139° 58′ 50,4″, S 21° 45′ 41,4″, Cme (sample nos 7262, 7263, 7275, 7280, 7282–4); (3) North of Rogers Ridge, E 139° 36,6′, S 21° 44′ 50,4″, Cmi (sample nos 7302–4, 7306–8, 7310, 7311, 7313, 7317, 7319, 7320); (4) About 1 km north of Mt Murray, E 139° 58′ 27,6″, S 21° 48′ 50,4″, Cme (sample nos 7321, 7322, 7324–6, 7328, 7331–45, 7347–50); (5) Phosphate Hill, excavation T15, E 139° 58′ 2″, S 21° 53′ 26″, Cme (sample nos 7351–9, 7362–7, 7371, 7374–6); (6) Phosphate Hill, excavation V9, E 139° 58′ 2″, S 21° 56′ 36″, Cme (sample nos 7377, 7383, 7390, 7393, 7394, 7400, 7401). (7) North of Rogers Ridge, E 139° 59,6′, S 21° 44′ 21″, Cmd (sample no. 7407), (8) North of Rogers Ridge, E 139° 59,6′, S 21° 44′ 19″, Cme (sample no. 7414); (9) Thorntonia, section 418, E 138° 53,8′, S 19° 7,4′, Cme (sample no 7464); (10) BMR Duchess 18, E 139° 59′ 16,4″, S 21° 45′, Cme (sample nos 7502, 7503).

Explanation of abbreviations: Cme, Monastery Creek Formation (late Templetonian); Cmi, Inca Shale (late Templetonian - ?early Floran; Cmc, Currant Bush Limestone (Undillan); Cmd, Devoncourt Limestone (Undillan) Ap, *Austroscolex primitivus*; As, *Austroscolex spatiolatus*; Cf, *Corallioscolex formosus*, Ep, *Euryscolex paternarius*; HoI, aff *H. oezguli* form species I, HoII, aff *H. oezguli* form species II, Kg, *Kaloscolex gravius*; Me, *Milaculum elongatum*; Mi, *Murrayscolex inaequalis*; Ms, *Murrayscolex serratus*; Po, *Pantoioscolex oleschinskii*, Rc, *Rhomboscolex chaoticus*; Sa, *Schistoscolex angustosquamatus*; Sm, *Schistoscolex mucronatus*; Su, *Schistoscolex umbilicatus*; Si, *Schistoscolex* sp. indet.; Sn, *Shergoldiscolex nodosus*; Sp, *Shergoldiscolex polygonatus*; Ta, *Thoracoscolex armatus*; Ha, cf. *Hadimopanella apicata*; Pi, Pal. gen. indet. sp. A

Locality	Age	Sample nos.	Ap	As	Cf	Ep	HoI	HoII	Kg	Me	Mi	Ms	Po	Rc	Sa	Sm	Su	Si	Sn	Sp	Ta	Ha	Pi
1 km N Mt Murray E 139° 58′ 27,6″, S 21° 48′ 50,4″	Cme	6958																					
Rogers Ridge, TP point E 139° 58′ 50,4″; S 21° 45′ 41,4″	Cme	7262		×										×	×		×						
		7263													×								×
		7275																					
		7280																					
		7282																					
		7283																				×	
		7284																					
N' Rogers Ridge E 139° 58′ 36,6″, S 21° 44′ 50,4″	Cmi	7302																					
		7303																					
		7304																					
		7306																					
		7307																					
		7308																					
		7310													×								
		7311																					
		7313																					
		7317																					
		7319																					
		7320																					
1 km N Mt Murray E 139° 58′ 27,6″, S 21° 48′ 50,4″	Cme	7321																					
		7322																					
		7324			×					×				×			×						
		7325																					
		7326	×												×								
		7328																					
		7331											×										
		7332													×	×							
		7333																					
		7334												×									
		7335		×						×		×		×			×		×	×			
		7336		×	×		×	×	×	×	×	×		×	×		×	×	×	×			
		7337						×		×	×	×			×		×				×		
		7338		×	×				×	×	×	×		×	×		×	×	×	×			
		7339		×		×	×		×	×				×	×				×	×	×		
		7340	×									×		×	×		×			×			
		7341		×											×								
		7342																					
		7343																					
		7344																					
		7345		×																			
		7347																					
		7348																					
		7349																					
		7350																					



TEXT-FIG. 1. Generalized geology of the northwestern Queensland Cambrian phosphogenic province (from Shergold and Southgate 1986).

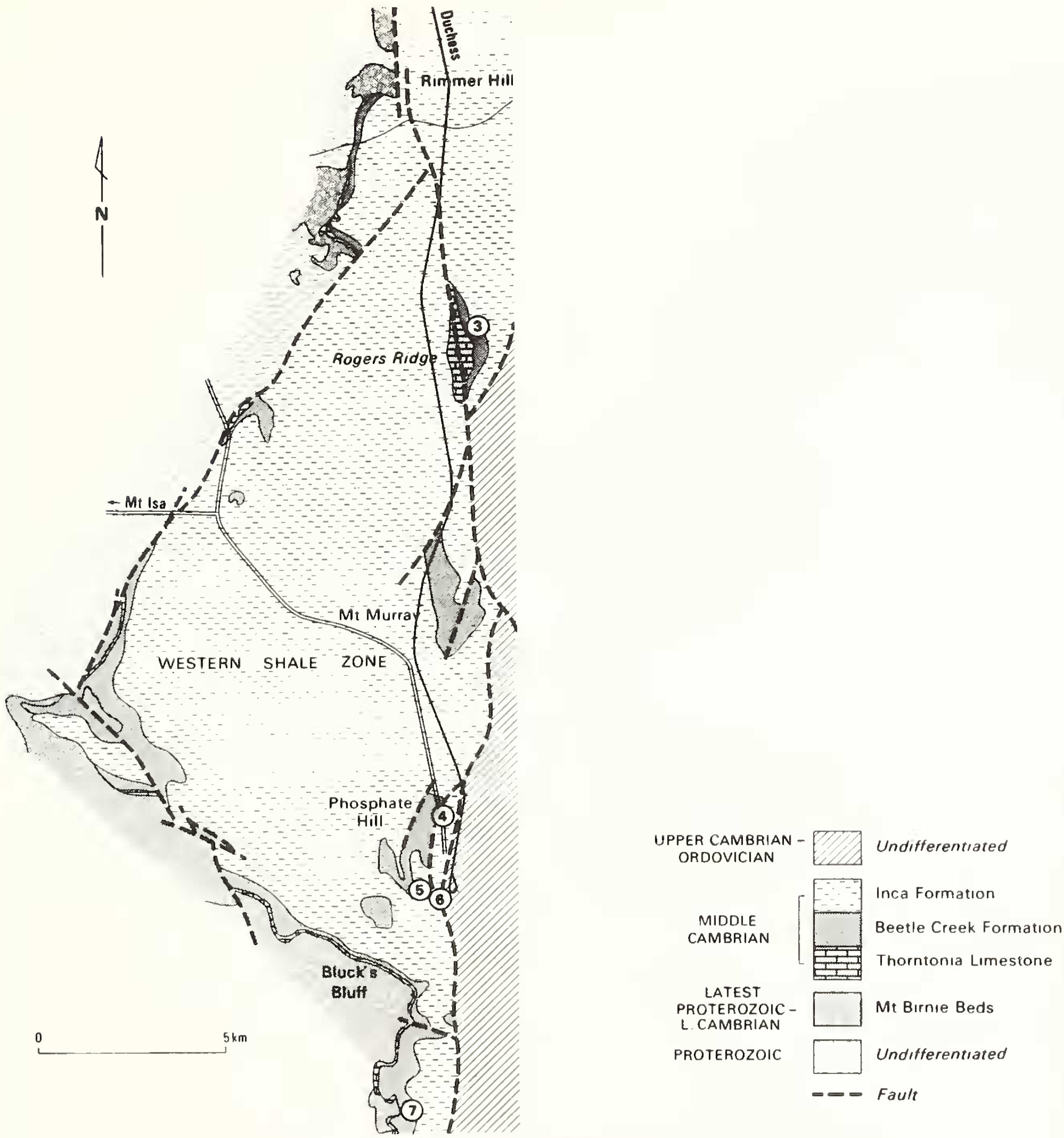
photography of the entire material would not have led to precise identifications because on many specimens the critical details are concealed by phosphatic precipitation. The number of specimens listed for each taxon is mainly based on photographed material only.

Outer morphological features have been documented using CamScanII photography. Internal structure was studied by thin-sections and observations of exfoliated fragments in transmitted light under a microscope. Measurements were obtained from the scanning photographs. The ratio between plates and platelets covering the surface has been calculated using the videoplan program by Contron on much-enlarged photographs.

Illustrated material is housed in the Commonwealth Palaeontological Collections of the Bureau of Mineral Resources, Canberra, under the numbers CPC 23001–23064.

STRATIGRAPHY

Middle Cambrian rocks extend virtually throughout the entire 325,000 km² of the Georgina Basin (Text-fig. 1). The succession is most complete in the southern and eastern parts. The sediments are rich in phosphate and, due to their economic importance, their investigation started in the 1960s (Shergold and Southgate 1986).



TEXT-FIG. 2. Phosphorite fields of the Duchess Embayment (from Shergold and Southgate 1986).

The present paper is based on material from the Thorntonia Region, the Duchess Embayment and the Ardmore Outlier (Text-fig. 2). Stratigraphically it can be assigned to the Templetonian and Floran stages.

In general Middle Cambrian sedimentation starts with arkose, conglomerates and detrital sands which may be fluvial. A dolomitic mudstone lithofacies passes into mudstone carbonates and coarser carbonates that are often associated with evaporites, phosphorites and siliceous sediments. These are followed by black shale and thin-layered carbonates or banked carbonates. The series terminates with more banked carbonates (for further details see Southgate and Shergold 1991).

The basal conglomerate of the Ordian is 2–75 m thick and is overlain by dolomitic lithofacies of the Thorntonia Limestone. This consists of recrystallized dolostones with wackestone and grainstone textures, followed by trilobite and echinoderm coquinites. At the end of the Ordian, the region faced a short period of emergence and subaerial erosion before rapid subsidence in the Early Templetonian led to the sedimentation of a chert-siltstone-phosphorite-limestone lithosome.

In the Thorntonia region the Bronco Stromatolithe marks the boundary between Ordian and Templetonian. Here, subsidence did not start before the late Templetonian. The type section of the Gowers Formation is 6·5 m thick and located at Section 418, southwest of Thorntonia Station. The basal part is formed by dolomitized phosphatic packstones. Subsequent lime-mudstones are followed by phosphatic wackestone and mudstone, capped by hardgrounds and phoscrete crusts.

The Ardmore Outlier is about 17 km west of Dajarra. The profile commences with the Riversdale Formation and the overlying Thorntonia Limestone that terminates with the Ardmore Chert. The Monastery Creek Formation follows disconformably in the early Templetonian. Its basal part, known as the Siltstone Member, is composed of thin-layered, siliceous phosphorites that are only poorly exposed in this area. The upper part of the Beetle Creek Formation, the Simpson Creek Phosphorite, is pelletal and well bedded with interbeds of collophane mudstone.

The Duchess Region is about 140 km southeast of Mt Isa and consists of several isolated phosphorite occurrences. They extend from Mt Birnie in the north to Phosphate Hill in the south. The outcrop at Rogers Ridge is situated within a series of en echelon faults at the northeast of the Duchess Embayment. The section exposes the Thorntonia Limestone, disconformably overlain by the Siltstone Member of the Monastery Creek Phosphorite Formation. It is differentiated into siliceous, calcareous and non-phosphatic facies. The calcareous facies consists of fetid, weakly dolomitic phosphatic limestone with micritic structure; chert and shale are minor components. The profile at the Trigonometric Point has a thickness of about 15 m and is formed by alternating layers of fossiliferous phosphatic carbonates, dolomite and cherts. They have been assigned to parasequence 2 of sequence 1 of the Monastery Creek Phosphorite Formation (Shergold and Southgate 1991) which is of late Templetonian age. Outcrops of the basal Inca Shale occur north of Rogers Ridge. It is composed of bleached bituminous shales with intercalated fossiliferous carbonate nodules. The presence there of *Triplagnostus gibbus* indicates a late Templetonian age. To the northwest, the shales pass into a laminated carbonate facies.

In the Mt Murray area, samples were collected as isolated, flat carbonate nodules that proved to be extremely fossiliferous. These also are of late Templetonian age. In contrast to the micrites at Rogers Ridge, the sediments here are sparry and bioclastic carbonates.

The Phosphate Hill deposits crop out about 15 km SSW of Rogers Ridge. Excavation T15 (Text-fig. 2; Localities 5 and 6) exposes a 11 m section showing ten lithological units (Shergold and Southgate 1986). The deposits of excavation V9 (Text-fig. 2; Locality 7) at the southernmost end of Phosphate Hill do not correlate easily with the recognized units of T15. Rogers and Crase (1980) therefore suggested an alphabetic division into units A–E. Mudstone phosphorite and chert are less abundant than at T15 and the series is heavily faulted.

A drill core (BMR Duchess 18) made northeast of Rogers Ridge provided samples from the Inca Formation which begins here prior to the late Floran *Euagnostus opimus* Zone. It thus can be regarded as a lateral equivalent of the Gowers Formation of the Thorntonia Region.

PRESERVATION

Notwithstanding their plated armour, Palaeoscolecida were originally soft and pliable, since occasional specimens are folded and some specimens show in part a narrow, high-relief annulation; it was the cuticle between the sclerotized parts that provided the elasticity. The material is preserved by secondary phosphatization, and traces of abrasion on the phosphatic coating indicate repeated transport. Most of the specimens were fragmented prior to final deposition and they give little evidence of the life position and ecology of the animals.

Between the individual samples there are considerable differences in completeness and mode of phosphatization. In some cases even the finest details are preserved, while in others a coarse coating may conceal otherwise distinct structures. Large worms are usually compressed, and due to compaction of the sediment, some specimens show interference between adjacent fossils. These differences in preservation are partly due to differences in sedimentation, and to dissolution and redeposition of phosphate in the deeply weathered sequences; the porous rock is an aquifer in some cases (J. H. Shergold, pers. comm.).

Almost complete specimens are rare and belong only to a few species. However, these specimens are usually thickly coated in phosphate; this cover prevented disintegration of the armour during entombment and during the etching process, but conceals details of the surface structure.

Our material comes from beds that contain many primary phosphatic sclerites, such as conodonts and horny brachiopods, together with other obviously secondarily phosphatized fossils, such as molluscs, 'ostracodes' and trilobites. As has been documented (e.g. Bengtson 1977; Bendix-Almgreen and Peel 1988), the sclerites are composed of two structurally different units: a fibrous core and brim, with organic fibrils between phosphatic material, and a dense phosphatic capping forming the surface ornamentation. According to the diagnosis given for *Lenargyrion* by Bengtson (1977), the sclerites were regarded as primarily phosphatic; we consider this quite likely. However, it seems that palaeoscolecidan sclerites have been discovered so far only from sediments in which secondary phosphatization occurred (e.g. Bengtson 1977, text-fig. 1A; Wrona 1982, pls 1–2; Peel and Larsen, fig. 2A–C; Hinz 1987, pl. 4, figs 3, 6; Bendix-Almgreen and Peel 1988, fig. 4A–C). The originally flexible cuticle of our palaeoscolecidan material is without doubt secondarily phosphatized. Despite the diagenetic origin of the phosphate, the lamellar wall structure is still observable in thin-sections (Text-fig. 17A–C). Therefore, the distinct structures of the sclerites cannot contribute to the question of whether the phosphatic nature is primary or diagenetic. This is in accordance with the opinion of Bengtson and Conway Morris (1984), who studied halkierid sclerites with regard to their original shell substance, and who stated that 'Although secondary phosphate itself normally shows amorphous structure, phosphatized specimens may preserve fine surface sculpture and internal structure of the wall'.

As isolated palaeoscolecidan remains have been studied in the past exclusively from residues prepared for conodont studies, a possible bias is suggested. If the palaeoscolecids had been calcareous they would have been dissolved during the preparation process. As far as we are aware, such remains have never been recovered by washing from soft clays. However, residues from such samples commonly are rather bulky, and conodonts concentrated by heavy liquid techniques before sorting. If not being actively sought in the smaller size-range, palaeoscolecidan remains may easily be overlooked in routine processing for conodonts by this method.

MORPHOLOGICAL CHARACTERS

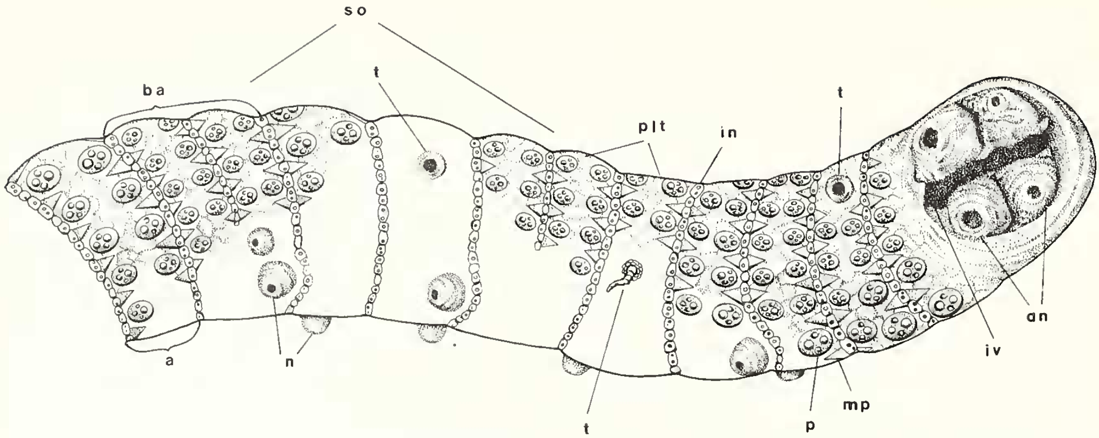
Our orientation of the worms has been based on the following.

1. In curved specimens, e.g. *Schistoscolex umbilicatus* (Text-fig. 11D), the convex side is considered as dorsal.
2. The distinction between oral and aboral end is based on specimens as shown in Text-figure 12B, D, G. The broken end on the inner side of the spiral (Text-fig. 11D) shows termination of the regular annulation of a broader portion; this suggests that the break would continue into the nippled aboral end (as shown, for example, in Text-figure 11B).
3. On fragments lacking both ends, the orientation was deduced from the inclination of the annuli according to principles of streamlining; the leading (stoss) side is considered to be oral, and the opposite (lee) side aboral. The sclerotized plates have a higher preservation potential than the whole animal. Accordingly they are common, and in many cases occur in great abundance. However, they show only a few of the relevant taxonomic characters of this group.

The platelets exhibit a wide range of shape. However, as isolated elements, they are generally small, and unidentifiable in the etched residues.

Characters of systematic value within the Palaeoscolecida (see Text-fig. 3) may be the following.

1. Number of rows of plates per annulus.
2. Rows that are distinguished by the size of the plates but not by their ornamentation.
3. Outline and ornament of individual plates.
4. Type of platelets (major or minor; with or without sculpture, rounded, polygonal or elongate; 'crumpled cuticle').
5. Arrangement of platelets (in rows, irregular etc.)



TEXT-FIG. 3. Morphological terms applied to palaeoscolecids. Abbreviations: a, annulus; an, aboral nipple; ba, bifurcated annulus; in, intercalation; iv, invagination; mp, microplate; n, nipple; p, plate; plt, platelet; so, indicated surface ornamentation; t, tubule.

TAXONOMIC CHARACTERS

The above-mentioned characters have been used for the generic and specific classification of the palaeoscolecids. However, a suprageneric taxonomy cannot be proposed because the characters used occur too variably in members of the group. Thus, the number of rows per annulus, the presence of intercalations, and the development of marginal rims of plates and platelets cannot be used to recognize families.

The study of ontogenetic stages was largely prevented by the fragmentary preservation; evolutionary trends could not be observed.

Worms having annuli composed of a double row of equally sized plates have ornamentation showing a mirror-image between the rows. Those with rows of differently-sized plates have the rows always placed in the same position (i.e. anterior or posterior) on the annulus. The position of platelets on annuli may be an additional specific character. Furcation of the annuli seems to be a taxonomically less important feature, because it is not essential for coiling, and in addition on a single specimen non-, bi-, and trifurcated ribs have been observed. The orientation of specimens broken both aborally and orally is sometimes recognizably the inclination of annuli towards the aboral end. Characters of isolated plates may be insufficient for specific identification because plates of the same form are found in different configurations and associations on different worms. For convenience it is suggested that new finds of such isolated sclerites should be published under open nomenclature.

SYSTEMATIC PALAEONTOLOGY

Phylum UNCERTAIN
Class PALAEOSCOLECIDA Conway Morris and Robison, 1986
Family PALAEOSCOLECIDAE Whittard, 1953

Discussion. The family comprises solitary worms with more-or-less rounded cross-sections but mostly with differentiated dorsal and ventral surfaces. Diameter of individual increases from anterior, may remain constant over quite a long distance distally but may slightly decrease again in that direction. Somewhat flexible multilamellar cuticle is armoured by skeletal plates. The capability of limited movements, such as contraction and relaxation, is documented in the different profiles of the annuli. The structure of the tissue is net-like and forms some sort of matrix for the insertion of the sclerites. Annulations are distinct and may be partly bi- or trifurcated on the dorsal side. On the same specimen, single rows may alternate irregularly with bi- or trifurcated rows (Text-fig. 11C). The outer skin of the annuli bear one to four rows of more-or-less regularly arranged plates. In between are much smaller platelets. Both are mineralized components but their primary substance is unknown; they were probably phosphatic. There is a certain variability in shape and adornment of the plates, particularly in respect to their position either on the dorsal or the ventral side. In some taxa, different morphotypes of plates have been observed which are generally arranged in alternating rows.

Ornamentation of plates and organization of the armour are considered as the main criteria for the recognition of species. A number of taxa have intercalations between the annuli that may have facilitated bending and other limited movements. These zones may form a zigzag band and have platelets that differ from those of the annuli in shape and arrangement.

The aboral end bears four nipples arranged in two lateral pairs. A longitudinal, slit-like opening between these pairs extends over the whole diameter of the worm. The slit opens towards an invagination.

Nipple-like protuberances similar to those at the aboral end may appear also on the ventral side, and are sometimes paired. Platelets are arranged concentrically around their bases, evidence that they are an original structure of the cuticle. Some specimens expose tubules (e.g. Text-fig. 5E–F) which may be also spread irregularly over the whole surface (Text-fig. 13A–B, F) and in this are similar to priapulids (Oeschger and Janssen 1991).

The oral end is usually broken. Even a well-preserved annulus cannot be regarded as the termination of the animal itself; it might represent the end of heavy armour passing into a proboscis similar to the 'unidentified worms' illustrated by Chen *et al.* (1991, fig. 7).

The soft body itself is not preserved on our material. Specimens flattened on shale frequently show a dark, narrow, longitudinal band extending over the entire length of the individual that may be interpreted as the gut. Glaessner (1979) even observed muscle fibres beneath the cuticle.

Size-range. Large, almost complete specimens of 0·10–0·15 m length have been observed only in shales. The length:width ratio of almost complete small specimens that were etched from limestones suggests a length of about 0·06 m for the largest, fragmentary individuals.

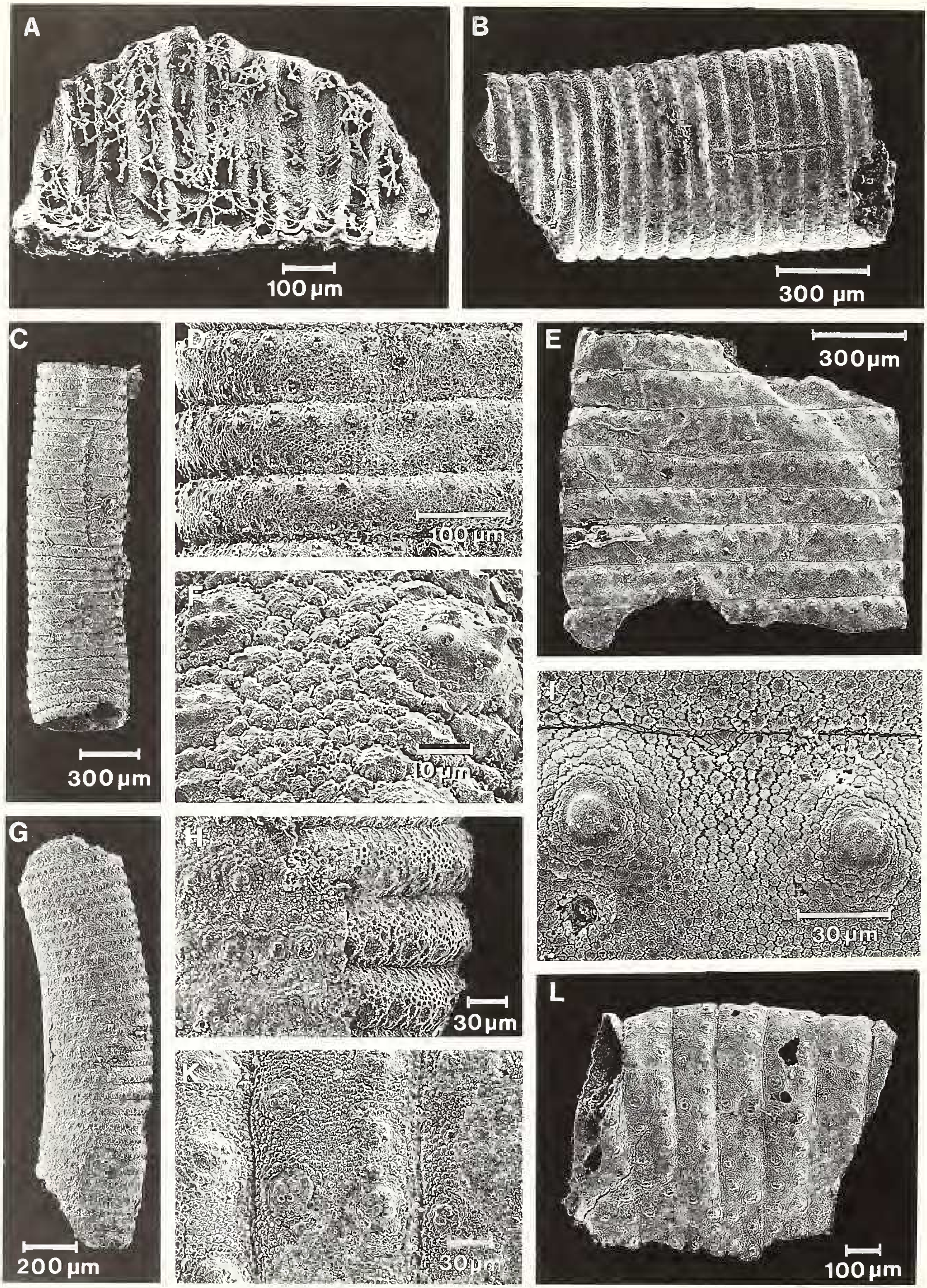
Occurrence and age. Lower Cambrian to Upper Silurian, Antarctica, Australia, China, Czechoslovakia, England, Estonia, Greenland, Siberia, Spain, Turkey, USA.

Genus AUSTROSCOLEX gen. nov.

Type species. Austroscolex spatiolatus sp. nov.

Derivation of name. Referring to its occurrence in Australia and *scolex*, Greek (worm).

Diagnosis. Annulation fairly broad, no intercalations. Annuli with widely spaced circular plates arranged in one or two rows. Median annular zone broad. Ornamentation of plates with central elevation that may differentiate into four or five nodes. Margins of plates and platelets jagged.


A
100 µm
B
300 µm
C
300 µm
D
100 µm
E
300µm
F
10 µm
G
200 µm
H
30 µm
I
30 µm
K
30 µm
L
100 µm

Austroscolex primitivus sp. nov.

Text-fig. 4E, I

Derivation of name. From *primitivus*, Latin, referring to the simple ornamentation.

Holotype. CPC 23006; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23006.

Other material. 14 specimens.

Diagnosis. Broad annulation with predominantly a single row of plates close to an annulus border.

Description. Isolated, laterally-compressed fragments of large worms. Annuli fairly broad and mainly with a single row of small plates that is located close to ?oral annulus border. Opposite side only occasionally with some plates. Second row only incompletely developed. Widely spaced plates with relatively large central elevation, and jagged margins of both plates and platelets similar to *A. spatiolatus*. Plates: platelets ratio about 1:2.

Austroscolex spatiolatus sp. nov.

Text-fig. 4C–D, F–H, K–L

Derivation of name. From *spatium*, Latin (space) and *latus*, Latin (broad) referring to the broad interspace between plates.

Holotype. CPC 23003; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23003–23005.

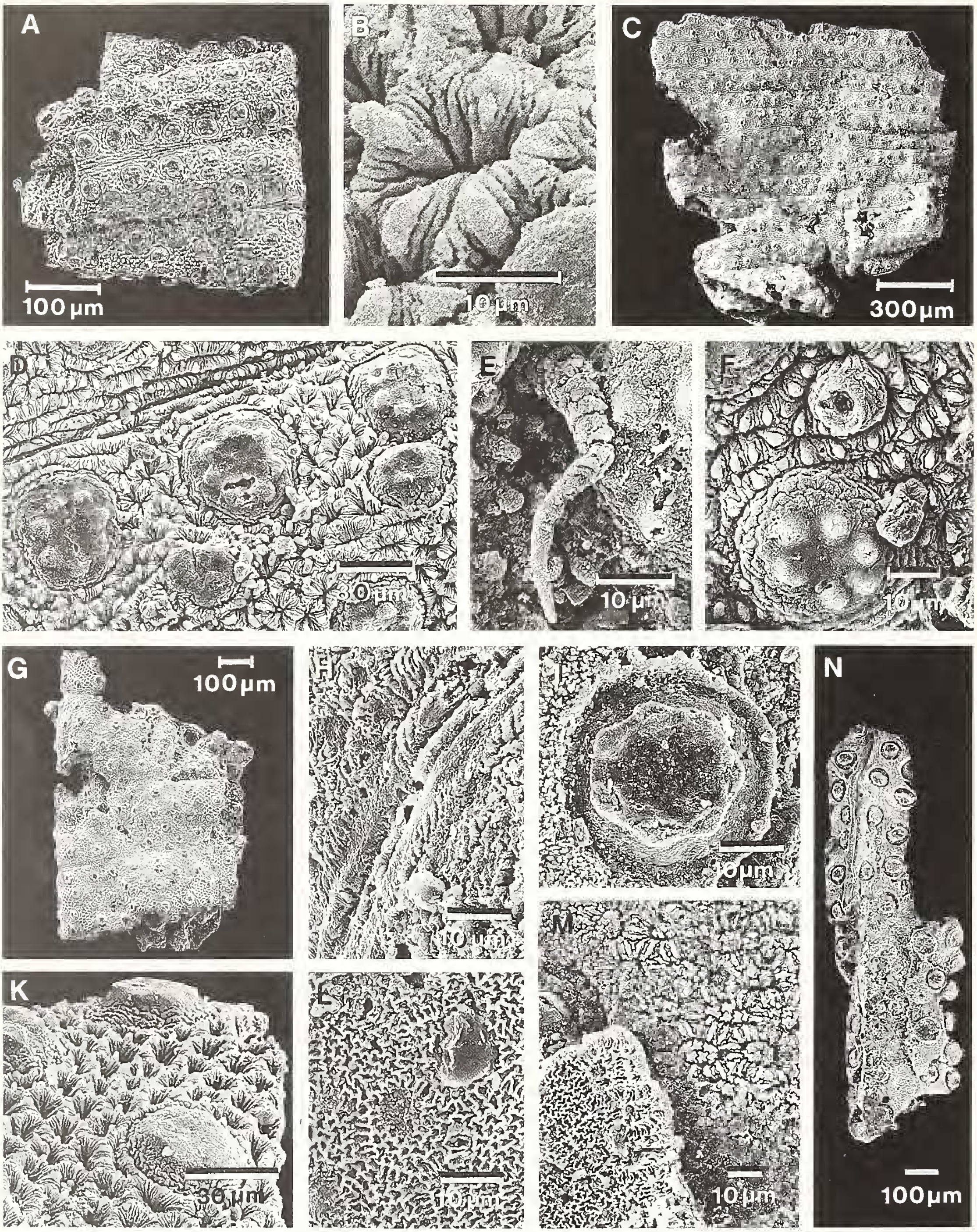
Other material. 67 specimens.

Diagnosis. Two rows of plates within an annulus; one row with smaller plates than the opposite row. Other characters as for the genus.

Description. Fragments of fairly large worms. Annulation quite regular with distinct apical inclination. Ornamentation of annuli with double row of widely spaced circular plates that differ considerably in size. Orally directed row bears comparatively smaller plates than opposite one. Distribution of plates within rows irregular and independent from each other. Plates with elevated centres with four small cones. Diameter of

---

TEXT-FIG. 4. A–B, Palaeoscolecida gen. et sp. indet. A, CPC 23001 (sample 7304); north of Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone; fragmentary specimen showing postmortal hypha-like threads on the inner surface, ×85. B, CPC 23002 (sample 7336); 1 km north of Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone; fragmentary specimen with distinct, longitudinal structure in the median plane, probably secondary, ×50. C–D, F–H, K–L, *Austroscolex spatiolatus* gen. et sp. nov. C–D, F, CPC 23003 (sample 7340), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. C, general view, ×30. D, detail of surface, ×150. F, detail of surface, ×900. G–H, CPC 23004 (sample 7262); Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone. G, general view, ×40. H, detail of surface; note matrix of exfoliated portion, ×215. K–L, CPC 23005 (sample 7262); Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone. K, detail of surface, ×235. L, general view, ×60. E, I, *Austroscolex primitivus* gen. et sp. nov., CPC 23006 (sample 7336), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. E, general view, ×50. I, detail of surface, ×500.



TEXT-FIG. 5. *Corallioscolex gravius* gen. et sp. nov. All specimens from 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone, except where otherwise stated. A–B, D, CPC 23007 (sample 7336), holotype. A, general view of fragment, ×110. B, detail of coralliomorph outer surface with radially arranged platelets, ×1900. D, detail of armour with irregularly distributed plates; note folds at annulus border, entire plate is about twice as wide as the centre. Marginal rim jagged. Platelets with irregularly polygonal outline and jagged margins. Upper surface topped by minute tubercles. Plates:platelets ratio about 1:4. On one specimen the uppermost layers of the cuticle are exfoliated and show a matrix in which the sclerites were anchored (Text-fig. 4H).

Comparison. The main differences between *Aaustroscolex primitivus* and *A. spatiolatus* are the incompletely developed second row of plates and the generally smaller size of the plates in *A. primitivus*, as well as the different upper surface of the plates.

Genus CORALLIOSCOLEX gen. nov.

Type species. Coralliöscolex gravius sp. nov.

Derivation of name. From *corallium*, Latin (coral), referring to the coralliomorph surface sculpture.

Diagnosis. Annuli with two to three rows of more-or-less equal plates. Intercalations not developed. Plates with distinct central depression, surrounded by several nodes. Platelets forming coralliomorph sculpture.

Coralliöscolex gravius sp. nov.

Text-fig. 5

Derivation of name. From *gravius*, Latin (beautiful) referring to the surface ornamentation.

Holotype. CPC 23007; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23007–23011.

Other material. 5 specimens.

Diagnosis. As for the genus.

Description. Fragments of large worms with broad annulation. Intercalations are lacking; instead, stretching of the worm exposes laminae between the annuli (Text-fig. 5H). Annuli ornamented by two to four rows of widely- and irregularly-shaped plates.

The plates vary in size and have a depressed centre surrounded by comarginal nodes. On a number of plates the surface seems to be almost completely abraded (Text-fig. 5K). Basal portion of plates appears as a girdle and consists of densely-spaced, irregularly polygonal platelets. Diameter of plate at its base is about one-and-a-half times larger than at the surface (Text-fig. 5I). The plate is embedded in a reticulate or cellular structure that appears as matrix for the overlying coralliomorph platelets (Text-fig. 5L–M).

The platelets form rosette-like, coralliomorph structures (Text-fig. 5B). They are composed of irregular, radially orientated blades, topped by larger, elongate sclerites with distinctly convex upper surface; four to six

---

×400. C, E–F, CPC 23008 (sample 7338). C, general view of large, fragmentary specimen, ×40. E, annulated tubule on outer surface, ×1150. F, detail showing plates, platelets and proximally broken tubules, ×800. G, K, CPC 23009 (sample 7336). G, general view, ×55. K, detail of outer surface with strongly abraded plates, ×465. H, CPC 23010 (sample 7324), Mt Murray, late Templetonian; surface detail showing stretched annulus border, ×950. I, L–N, CPC 23011 (sample 7338). I, surface detail of single plate; the broad basal portion and part of the girdle were originally covered by secretory tissue, ×950. L, detail of inner layers with both coralliomorph and labyrinthic structure; an exfoliated portion has been accidentally attached to the coralliomorph surface, ×950. M, detail of surface showing structure of an underlying layer with labyrinthic structure, ×500. N, general view of fragment, ×50.

of these sclerites are positioned on each rosette as radiating septa-like structures. Margins of platelets are partly jagged. Plates: platelets ratio about 1:4 or 1:3.

Another characteristic of the cuticle is the presence of tubules that seem to be annulated proximally (Text-fig. 5E).

Genus EURYSCOLEX gen. nov.

Type species. Euryscolex paternarius sp. nov.

Derivation of name. From *eurys*, Greek (broad) referring to the broad median annular zone.

Diagnosis. Broad annulation, no intercalations. Annuli with three to four rows of widely-spaced plates. Concave upper side of plates with radial sculpture. Platelets with jagged outer margin.

Euryscolex paternarius sp. nov.

Text-fig. 15A–D

Derivation of name. From *patera*, Latin (bowl), referring to the shape of the sclerites.

Holotype. CPC 23053; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23052–23053.

Other material. 4 specimens.

Diagnosis. As for the genus.

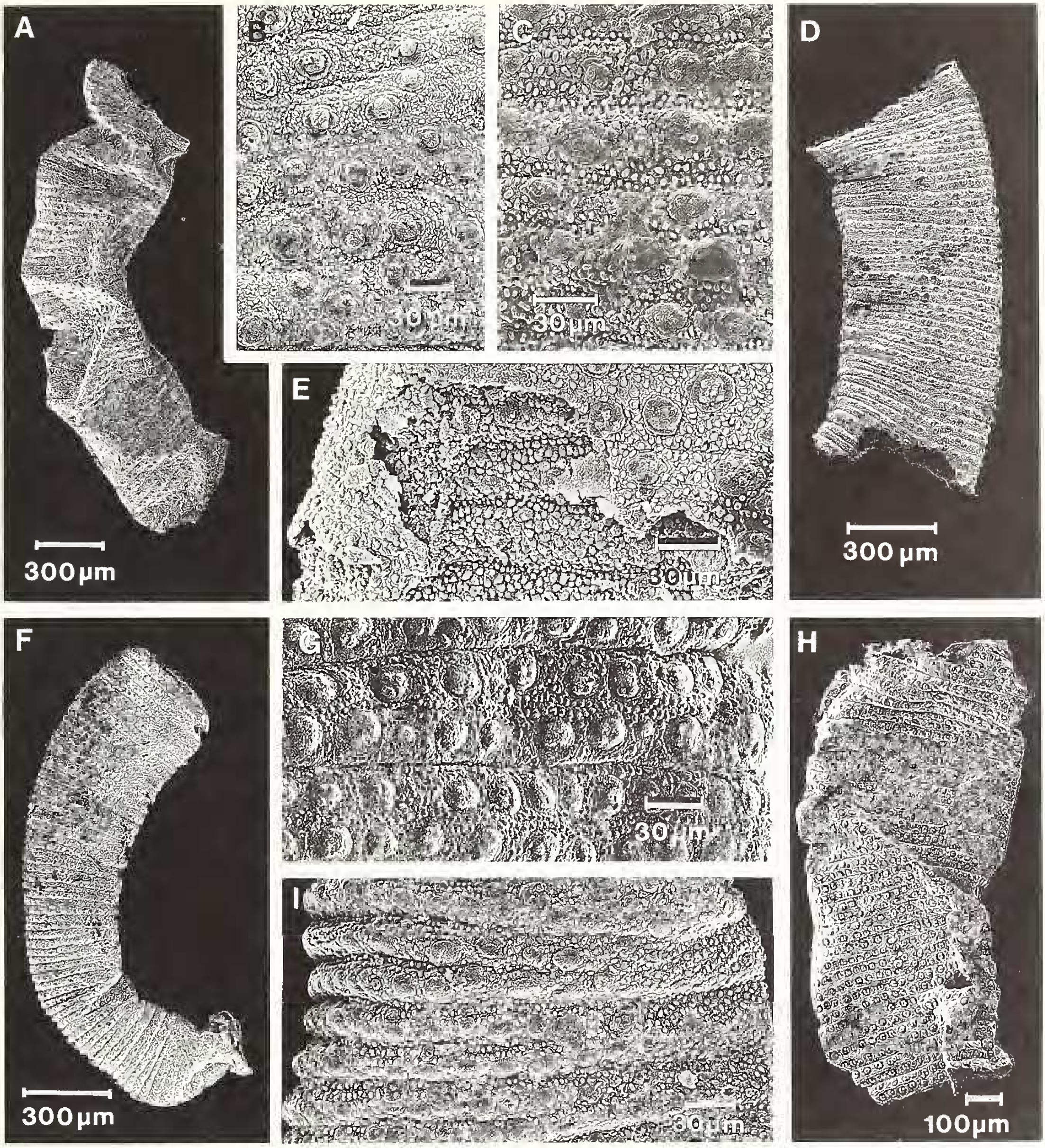
Description. Wall fragments of large worms, with annulus borders indicated only by narrow furrows. Intercalations not observable. Annuli with flat relief and widely- but irregularly-spaced plates of different size. Proper rows not distinguishable. Plates circular, depressed centre with faint radial ribbing. Margin elevated and smoothly scalloped, topping a steep girdle with comparatively coarse vertical ribs. Platelets tiny, with jagged margins, surface differentiation not recognizable; arranged in a distinct mosaic pattern of larger polygonal units that are, however, still much smaller than the plates (Text-fig. 15D). Plates: platelets ratio about 1:4.

Genus HADIMOPANELLA Gedik, 1977

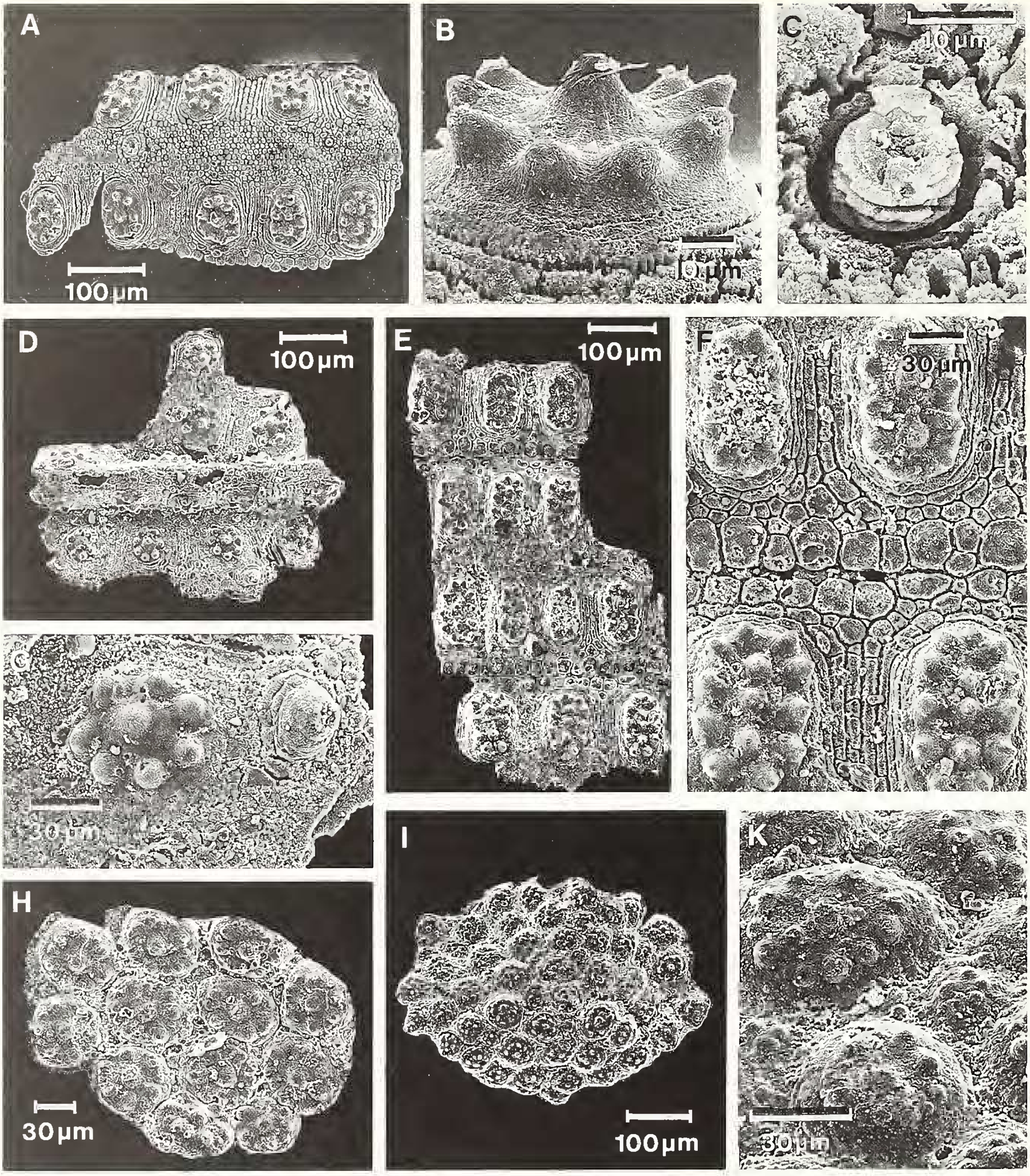
Type species. Hadimopanella oezguli Gedik, 1977.

Diagnosis (after Gedik 1977, 1989). A phosphatic circular unit with strongly convex upper surface decorated by tubercles in its central part and a slightly convex to plane and smooth lower surface. The tubercles are coarse, i.e. greater than 10 μm and regularly distributed. Most tubercles are on the outer circular row and a few on the central part. The tuberculated area forms about half of the full diameter. The non-tuberculated marginal area, called marginal brim, is broad. The height: diameter ratio is about 1:3.

Remarks. Sclerites similar to *Hadimopanella oezguli* were discovered in two different configurations which, from what is known of other more complete worms, probably characterize different taxa. As they are represented only by one or two fragments, they are described herein as form species I and II.



TEXT-FIG. 6. *Kaloscolex granulatus* gen. et sp. nov. All specimens from 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A–B, CPC 23012 (sample 7338). A, general view of terminally broken and wrinkled specimen, × 30. B, detail of surface; note irregular distribution of plates, × 215. C–D, CPC 23013 (sample 7336). C, surface detail; note ornamentation of platelets, × 300. D, general view of specimen, × 40. E, CPC 23014 (sample 7339); surface detail showing underlying layer with less distinct plates and more closely-spaced platelets, × 300. F, I, CPC 23015 (sample 7338), holotype. F, lateral view, × 40. I, detail showing strong annular relief and furcation of ribs on dorsal side; ventral side flattened; ratio of platelets: plates increased in this portion, × 235. G–H, CPC 23016 (sample 7338). G, surface detail of armour, × 265. H, general view of large, deformed specimen, × 50.



TEXT-FIG. 7. A–C, E–F, *Milaculum elongatum* sp. nov. A–C, CPC 23017 (sample 7336); 1 km north of Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. A, general view of fragment representing about the width of an annulus; note elongate platelets between plates, ×110. B, profile of single plate with fine radial ribs and jagged outer, basal margin, ×800. C, surface detail with broken tubule, ×1550. E–F, CPC 23018 (sample 7336), holotype; 1 km north of Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. E, piece of large specimen with broad, flat annuli, ×100. F, detail showing ornamentation of plates and mosaic pattern of platelets, ×285. D, G, aff. *Hadimopanella oezguli* form species I; CPC 23019 (sample 7324); Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. D, fragmentary, deformed specimen, ×95. G, detail of surface with plate and adjacent nipple-like protuberance, ×365. H–K, aff. *Hadimopanella oezguli* form species II. H, CPC 23020 aff. *Hadimopanella oezguli* Gedik, 1977

1977 *Hadimopanella oezguli* Gedik, p. 46, pl. 5, figs 1–5.
1988 *Hadimopanella oezguli* Gedik; Märss, p. 14, pl. 1, figs 1–8.
1989 *Hadimopanella oezguli* Gedik; Gedik, p. 69, pl. 1, figs 1–2.
1990 *Hadimopanella oezguli* Gedik; Hinz *et al.*, fig. 1D.

Form species I

Text-fig. 7D, G

Material. Figured specimen, CPC 23019.

Description. Piece of armoured cuticle with terminations and cross-section indeterminable. Annulation fairly broad, intercalations not recognizable. Each annulus with a double row of equal plates. They have nearly the same size and are approximately regularly arranged with distinct interspaces between them. Plates rounded, with a circle of 6 or 7 marginal nodes and a central node that may be somewhat larger. Platelets polygonal in the middle of the annuli; between plates, platelets are elongate and extending parallel to long axis of the worm. All platelets have jagged margins that are particularly obvious close to the underside. The surface is further characterized by tubules.

Remarks. This form seems to be similar to *Palaeoscolex sinensis* Hou and Sun, 1988, from the Lower Cambrian Cheng-jiang fauna with *Eoredlichia*, in which the plates are similarly arranged and ornamented, but the illustrations do not show the critical details. Furthermore, the authors state a double row of ribs in the median zone of each annulus; by contrast *Hadimopanella oezguli* has polygonal platelets. The latter feature, however, may be preservational; this can be confirmed only by having suitable material at hand.

Form species II

Text-fig. 7H–K

Material. 2 specimens, CPC 23020–23021.

Diagnosis. Cuticle with densely-spaced plates. Border of annuli indistinct.

Description. Piece of wall of a large specimen. Annulation indistinct. Surface is covered by densely-spaced, rounded plates. Surface of plates distinctly convex with central node encircled by further nodes of the same size. Narrow interspace between plates filled with rounded, nodular platelets.

Genus KALOSCOLEX gen. nov.

Type species. Kaloscolex granulatus sp. nov.

Derivation of name. From *kalos*, Greek (beautiful) referring to the surface ornamentation.

Diagnosis. Annulation dense, partly furcated. Intercalations lacking. Annuli with one to two rows of plates; upper surface of plates with four to five nodes. Platelets with median elevation leading to a granular appearance of the cuticle.

(sample 7337); 1 km north of Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone; piece of armoured cuticle with indistinct annulation, ×200. I, K, CPC 23021 (sample 7336); 1 km north of Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. I, piece of densely armoured cuticle, ×90. K, detail with ornamentation of plates and microplates, ×490.

Kaloscolex granulatus sp. nov.

Text-fig. 6

Derivation of name. From *granulatus*, Latin, referring to the granular ornamentation of platelets.

Holotype. CPC 23015; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23012–23016.

Other material. 3 specimens.

Diagnosis. As for the genus.

Description. Curved specimens with slight increase in diameter towards oral end; cross-section undeterminable, intercalations lacking. Annuli partly with furcation on the convex side; accordingly, the ornamentation differs between convex and concave sides: the convex face displays plates, the concave side exposes only irregular platelets and erratic pillars (Text-fig. 6I). According to the curvature, the convex side is regarded as dorsal, and the concave side as ventral.

Annuli ornamented by an irregular arrangement of widely spaced plates in one or two approximate lines. Sometimes, smaller plates are randomly added. Size of plates highly variable, outline crudely rounded with irregular margin. Plates with four to five nodes around the centre.

Platelets of two types: (a) oval sclerites, with distinct median elevation, more-or-less concentrically arranged around plates; (b) smaller, polygonal to elongate platelets with irregular margin, surrounding the first type.

On exfoliated specimens, i.e. on a lower level of the cuticle, the convex platelets (type a) are more densely-spaced. Plates are recognizable only in an incipient stage (Text-fig. 6E). Plates:platelets ratio about 1:1.

Tubules situated on the lateral face appear segmented.

Genus MILACULUM Müller, 1973

1989 *Plasmuscolex* Kraft and Mergl, p. 25.

Type species. *Milaculum ruttneri* Müller, 1973.

Milaculum elongatum sp. nov.

Text-fig. 7A–C, E–F

Derivation of name. From *elongatus*, Latin, referring to the shape of the plates.

Holotype. CPC 23018; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23017–23018.

Other material. 43 specimens.

Diagnosis. Annulation very broad and flat; intercalations lacking. Annuli with two rows of plates ornamented by vertical rows of nodes. Elongate platelets between individual plates of one row. Median annular zone and border of annuli with polygonal platelets.

Description. Fragmentary large worms with fairly wide annuli; intercalations lacking. Ornamentation of annuli with two rows of elongate plates arranged along the borders of each annulus. Spacing of plates distinct and regular.

Plates subsymmetrical with elongate to oval outline and tapering very slightly towards the central area of each annulus. Outer margin of plates smooth. Sculpture with comarginal, outwardly directed nodes or cones.

One to three median cones may be present even within the same row of an annulus. A faint radial ribbing is observable (Text-fig. 7B).

Platelets rather small in comparison with the large plates. Regarding their outer shape, two types of platelets are developed: polygons, and narrow, elongate platelets. Towards the borders of each annulus, relatively large polygonal platelets are present; by contrast, in the central area there are only small polygons. Between the plates there are elongate platelets reflecting the outline of the plates. Up to about ten longitudinal rows of platelets have been observed between two plates (Text-fig. 7A). All sclerites have minutely jagged outer margins (Text-fig. 7B). Plates: platelets ratio about 2:1.

Remarks. There is some similarity to *Hadimopanella oezguli* in the presence of elongate platelets between the plates, but shape and ornamentation of plates are distinctly different.

Genus MURRAYSCOLEX gen. nov.

Type species. Murrayscolex serratus sp. nov.

Derivation of name. From its occurrence at Mt Murray, Queensland.

Diagnosis. Annulation moderately broad, intercalations lacking. Annuli with two rows of alternating plates, one row with larger plates than the opposite row. Upper surface of plates nodular, outer margin jagged. Microplates between plates in one row.

Murrayscolex inaequalis sp. nov.

Text-fig. 8D–F

Derivation of name. From Latin, referring to the unequal development of plates in both rows of an annulus.

Holotype. CPC 23026; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

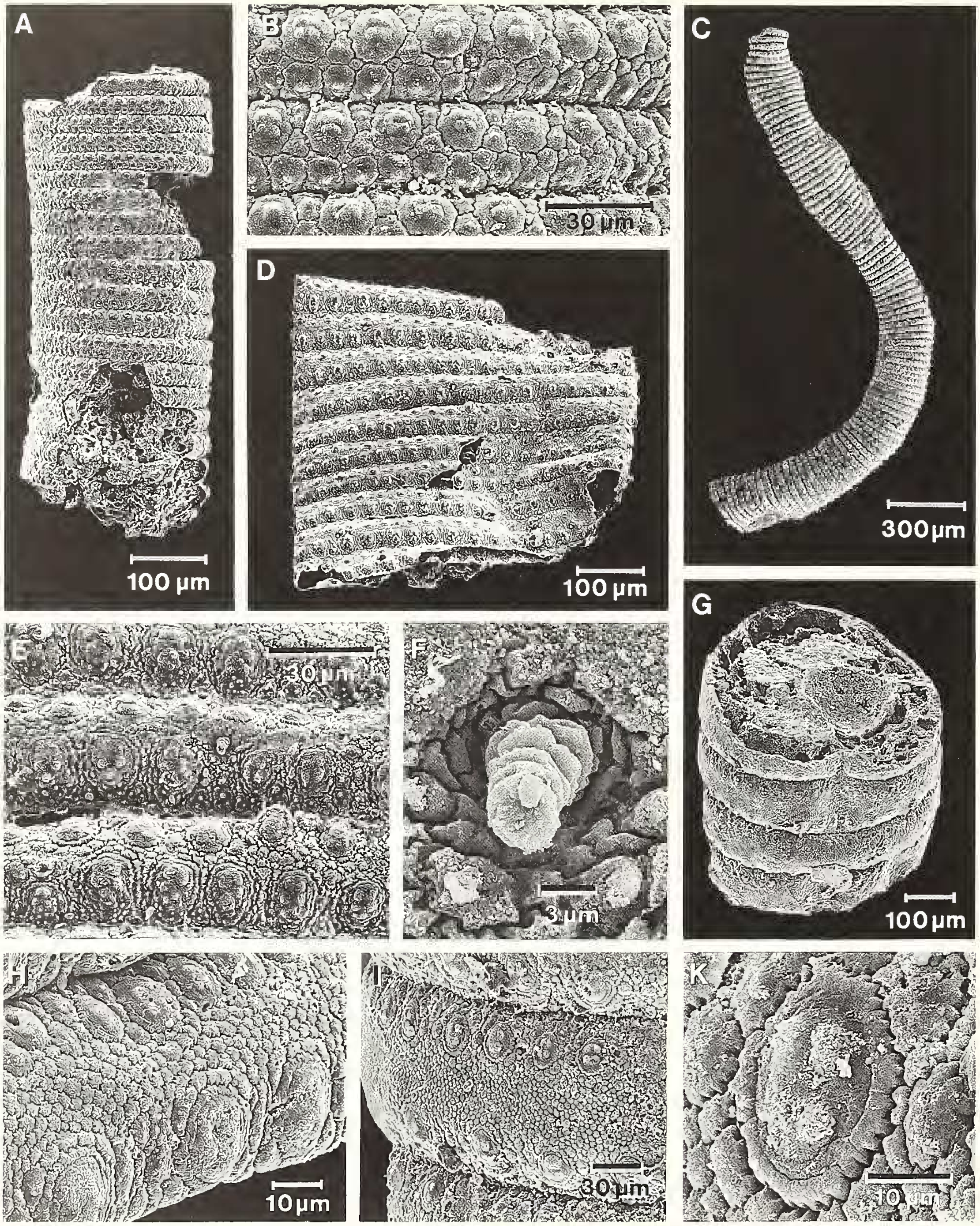
Illustrated material. CPC 23026.

Other material. 2 specimens.

Diagnosis. Shape of plates tapering towards respective annulus borders. Upper surface of plates and microplates highly ornamented. Other characters as for the genus.

Description. Parts of very large worms; annulation fairly broad, intercalations lacking. Ornamentation of annuli with two rows of plates, one row with larger and more elongate plates than the opposite row. Elongate plates quite closely spaced; towards centre of annulus they are broadly rounded, tapering slightly towards its border. Broader portion with up to six fairly large nodes, smaller area with numerous tubercles that may also be comarginal. Between plates, smaller, subtriangular microplates with tuberculate surfaces are intercalated. Opposite rows with smaller, rounded plates of similar ornament and with microplates between. Interspace filled by irregular platelets with jagged margins. Plates: platelets ratio about 3:1. On one specimen (Text-fig. 8E–F) a distinct, segmented protuberance is visible.

Remarks. This form differs from *Murrayscolex serratus* mainly in the development of the larger plates with their differentiated outer shapes and a tuberculated terminal zone, and in the narrower central area of the annuli.



TEXT-FIG. 8. *Murrayscolex* gen. nov. A–C, G–K, *Murrayscolex serratus* sp. nov. A–B, CPC 23022 (sample 7390), holotype; Phosphate Hill, excavation no. 9, late Templetonian, *Triplagnostus gibbus* Zone. A, general view, ×115. B, detail of armour, ×535. C, CPC 23024 (sample 7337); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone; lateral view of curved specimen with broken aboral and oral ends,

Murrayscolex serratus sp. nov.

Text-fig. 8A–C, G–K

Derivation of name. From *serratus*, Latin, referring to the jagged margin of sclerites.

Holotype. CPC 23022; from Phosphate Hill, excavation no. 9, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23022–23025.

Other material. 2 specimens.

Diagnosis. Plates close to annulus borders. Ornamentation of plates with elevated centre, encircled by tubercles. Median annular zone variable in width.

Description. Large fragments without preserved oral and aboral ends; cross-section nearly circular. Annulation broad and fairly regular with convex dorsal and flattened ventral relief. Ornamentation of annuli with two rows of irregularly alternating plates positioned close to borders of annuli. Rows are distinguished only by the size of the plates. Plates rounded to elongate with three to four larger, partly fused central nodes, encircled by minute, irregularly-spaced nodes. Towards annulus border, the nodular row may be doubled. Plates generally highly variable in size and ornament. Microplates, with sculpture similar but not identical to plates, are positioned between the plates and along borders of annulus. Platelets developed as small polygons with convex, hardly differentiated upper surface. They are positioned in central zone of annulus. Platelets within intercalations are oval-shaped with multinodular surface. Both plates and platelets have jagged margins. Plates:platelets ratio about 1:1 (Text-fig. 8A) or 1:2 (Text-fig. 8G–K).

Genus PANTOIOSCOLEX gen. nov.

Type species. Pantoioscolex oleschinskii sp. nov.

Derivation of name. From *pantoios*, Greek (of all sorts) referring to the high variability in size of the sclerites.

Diagnosis. Ornamentation consisting of narrow rows of small plates alternating with zones of more densely-spaced microplates. Ornamentation of sclerites with four to six nodes. Annulus borders indistinct.

Pantoioscolex oleschinskii sp. nov.

Text-fig. 16A, C

Derivation of name. In honour of Mr Georg Oleschinski, Bonn.

Holotype. CPC 23057; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

×40. G, I, K, CPC 23023 (sample 7350); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. G, oblique view from above, ×75. I, details of armour, ×265. K, detail of armour, ×490. H, CPC 23025 (sample 7335); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone; surface detail of specimen with strongly abraded plates, almost down to planation, ×750. D–F, *Murrayscolex inaequalis* sp. nov. CPC 23026 (sample 7336), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. D, general view of large, compressed fragment, ×100. E, detail of ornamentation with more or less triangular microplates between plates, ×550. F, surface detail with annulated tubules, distally broken-off, ×3000.

Material. Figured specimen, CPC 23057.

Diagnosis. As for the genus.

Description. Large fragment of a single specimen that differs from all other taxa in its surface pattern. Annulus borders indistinct, relief flat. Ornamentation with narrow rows of small plates in somewhat irregular arrangement alternating with broad zones of more densely-spaced microplates. Sclerites highly variable in size, and surface topped with circle of four to six nodes. Interspaces smooth, platelets not recognizable. Plates:interspace ratio about 1:2.

Remarks. With regard to the surface pattern, there is superficial similarity between *Pantoioscolex oleschinskii* and *Palaeoscolex antiquus* Glaessner, 1979. Both taxa show an alternation between rows of larger plates and comparatively broad zones with smaller, densely spaced plates.

Conway Morris and Robison (1986) presented drawings of the ornamentation patterns of *Palaeoscolex piscatorum* Whittard, 1953, *P. ratcliffei* Robison, 1969 and *P.* cf. *ratcliffei* Conway Morris and Robison, 1986, as well as *P. antiquus* Glaessner, 1979. A paratype of *P. piscatorum* (RU 4200 and RU 4200 counterpart) in the collections of the British Geological Survey, shows a net-like sculpture comparable to Whittard's illustration (Whittard 1953, pl. 5, fig. 2). It is similar to the matrix illustrated on exfoliated specimens (e.g. Text-fig. 4H) and suggests that not the outer surface but an inner layer is exposed. As has been shown for *Kaloscolex granulatus* (Text-fig. 6E), the sculpture may differ considerably between outermost and inner layers. Therefore, *P. piscatorum* is unsuitable for direct comparison.

Genus RHOMBOSCOLEX gen. nov.

Type species. Rhomboscolex chaoticus sp. nov.

Derivation of name. From *rhombus*, Latin, referring to the surface ornamentation by platelets.

Diagnosis. Broad, flat annulation with two rows of widely spaced plates. Intercalations lacking. Ornamentation of plates with circle of tear-shaped nodes around central depression. Platelets forming a superficial rhombic pattern, particularly in broad, central area of annuli.

Rhomboscolex chaoticus sp. nov.

Text-fig. 9

Derivation of name. From *chaos*, Latin, referring to the chaos theory and the repetition of non-identical structures.

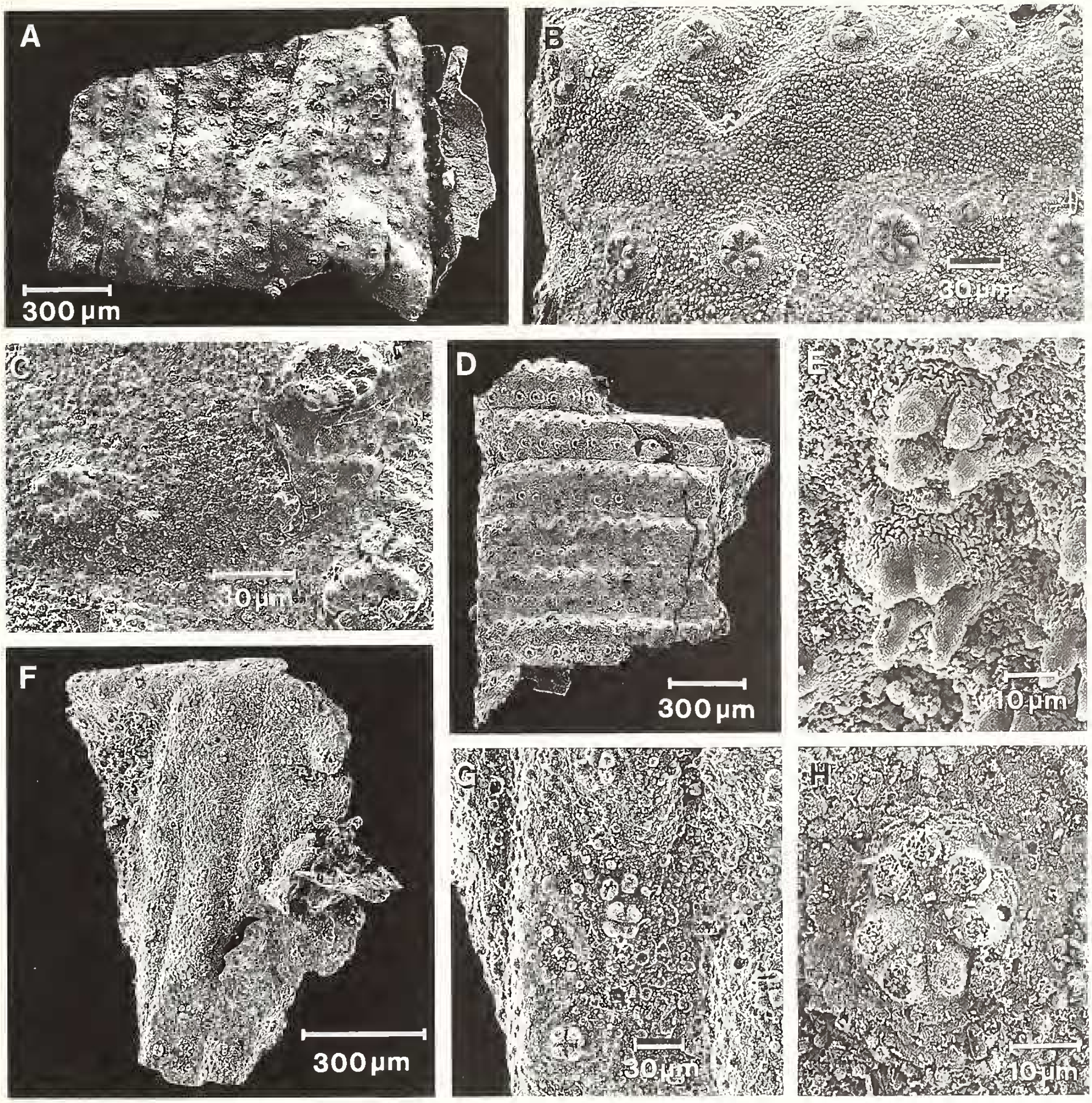
Holotype. CPC 23028; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23027–23030.

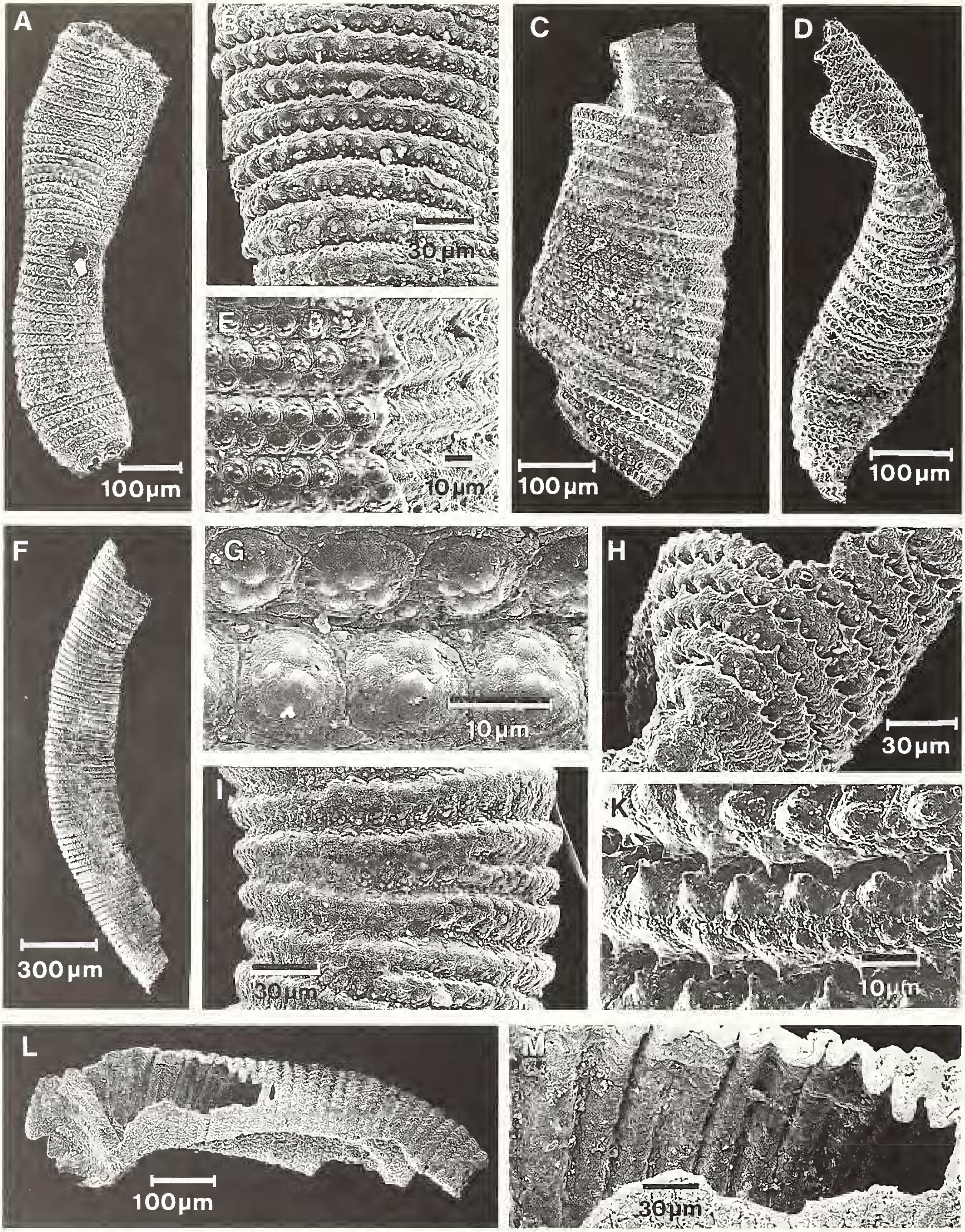
Other material. 3 specimens.

Diagnosis. As for the genus.

Description. Laterally compressed fragments of large individuals without preserved oral and aboral ends. Annuli somewhat variable in width but generally fairly broad and without pronounced relief. Annuli with two widely spaced rows of unequal plates, each row close to either border. Although highly variable in size, plates are generally larger in one row than in the opposite row.



TEXT-FIG. 9. *Rhomboscolex chaoticus* gen. et sp. nov. A, C, CPC 23027 (sample 7340); Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone. A, general view of large, compressed fragment, ×40. C, detail of annulus ornamentation; note different size of plates, ×365. B, D, CPC 23028 (sample 7338), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. B, surface detail with platelets forming a superficial rhombic pattern, ×250. D, general view of specimen, ×35. E–G, CPC 23029 (sample 7324); Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. E, surface detail of exfoliated portion exposing crumpled cuticular structure at the base of the sclerites; plates ornamented with four high cones, ×700. F, general view of specimen, ×55. G, surface detail; here the rhombic pattern is stressed by larger nodes on each corner, ×215. H, CPC 23030 (sample 7339); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone; surface detail of specimen in which the plate has its girdle exfoliated, ×950.



TEXT-FIG. 10. *Schistoscolex* gen. nov. A–C, E–G, I, L–M, *Schistoscolex angustosquamatus* sp. nov. A–B, CPC 23031 (sample 7336), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A, ventrolateral view of specimen with preserved aboral portion, ×95. B, detail of surface ornamentation, Plates rounded to oval-shaped with depressed centre encircled by tear-shaped nodes, which are arranged in rosettes with inwardly directed tips. Girdle steep and passing into a flattened brim with jagged margin. Plates are encircled by several rows of platelets (Text-fig. 9B).

Platelets are generally quite uniform, rounded to polygonal, partly with jagged margins, strongly convex and developed in two size-orders. Larger platelets appear to build a trellis ornament. Superficial rhombic arrangement sometimes stressed by larger, almost globular platelets topping the corners of each rhomb (Text-fig. 9G). On a small portion of a single specimen, plates are extremely densely-spaced and ornamented by four to five strikingly high cones (Text-fig. 9E–F). The significance of this feature is uncertain.

In general the outer layer consists of convex platelets beneath which a crumbled cuticular structure is observable on a partly exfoliated specimen (Text-fig. 9E). Plates: platelets ratio about 1:4.

Remarks. Although the rhombic structure appears consistent, closer inspection reveals that every rhomb differs from the adjacent rhombs, which is not due to deformation, but is a primary feature. In chaos theory the term fractal has been used for such a pattern which does not repeat itself.

Most of the specimens have a considerable phosphatic coating that conceals the fine original structures.

Genus SCHISTOSCOLEX gen. nov.

Type species. Schistoscolex umbilicatus sp. nov.

Derivation of name. From *schistos*, Greek (separate), referring to the furcation of annuli.

Diagnosis. Annulation narrow, partly furcated. Intercalations small. Annuli with two rows of relatively large plates in contact with each other. Surface of plates with one to four larger nodes. Marginal tubercles may be developed towards annulus borders.

Schistoscolex angustosquamatus sp. nov.

Text-fig. 10A–C, E–G, I, L–M

Derivation of name. From *angustus*, Latin (narrow), and *squamatus*, Latin (adorned with plates), referring to the dense arrangement of plates.

Holotype. CPC 23031; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23031–23035.

Other material. 8 specimens.

×300. C, E, G, CPC 23032 (sample 7310), holotype; north of Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone. C, general view of fragmentary specimen, ×115. E, surface detail showing exfoliated portion with matrix for the insertion of plates, ×400. G, surface detail with plates along annular border, ×400. F, CPC 23033 (sample 7341); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone; lateral view of specimen with rather irregular annulation, ×40. I, CPC 23034 (sample 7262); Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone; detail of specimen showing dorsal bifurcation of ribs, ×350. L–M, CPC 23035 (sample 7337); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. L, general view of fragmentary specimen, ×100. M, detail showing inner surface and strongly folded (contracted) profile of ribs, ×285. D, H, K, *Schistoscolex mucronatus* sp. nov., CPC 23036 (sample 7332), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. D, general view of fragmentary and deformed specimen, ×125. H, detail showing strongly aborally inclined spines, ×365. K, detail of armourment with alternating spiny plates, ×900.

Diagnosis. Annulation narrow, partly furcated; intercalations indistinct. Plates densely arranged, ornamentation with one or two, large, inclined central nodes. Smaller nodes may be present towards annulus border.

Description. Curved individuals with circular cross-section. Annulation narrow, partly bifurcated. Intercalations indistinct. Each annulus with two rows of large plates forming an acute angle along the median plane in the contracted condition of the worm (Text-fig. 10E). Plates in close contact with each other. Elevated central part of plates with four to five irregular nodes or cones, differentiating into one larger node positioned towards the midline of the annulus and pointing to the annulus border. Several smaller and irregular nodes at opposite side. The smaller nodes of the sclerites are always positioned along the annulus borders, the larger nodes are developed in the middle of the annuli. Platelets are only developed as fillings of the small interspaces. Their shape is thus dependent on the space available and appears irregularly elongate. Between the plates, towards the annulus borders, there is a roughly oval to triangular platelet with a distinct median node (Text-fig. 10G). Plates: platelets ratio about 9:1.

Remarks. There are similarities in the furcation of ribs, and arrangement and density of plates between *Schistoscolex angustosquamatus* and *S. umbilicatus*. The main difference between the two species is the inclined subcentral node in *S. angustosquamatus*.

Schistoscolex mucronatus sp. nov.

Text-fig. 10D, H, K

Derivation of name. From *mucronatus*, Latin (adorned with a spine or thorn), with reference to the spine-like subcentral node.

Holotype. CPC 23036; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23036.

Other material. 1 specimen.

Diagnosis. Plates smaller than in other species; microplates irregularly distributed in central annular zone. Ornamentation of plates with large, spine-like central elevation. Other characters as for the genus.

Description. Fragmentary worms without preserved aboral and oral ends. Width of annuli somewhat variable, convexity depending on degree of contraction. Intercalations not recognizable. Ornament of annuli with two rows of alternating, relatively large, closely-spaced plates. Towards the border, a submedian, spine-like cone is surrounded by a few nodes. The central zone of each annulus may be filled by polygonal to irregular platelets or microplates that share the ornament with the plates. Plates: platelets ratio about 9:1.

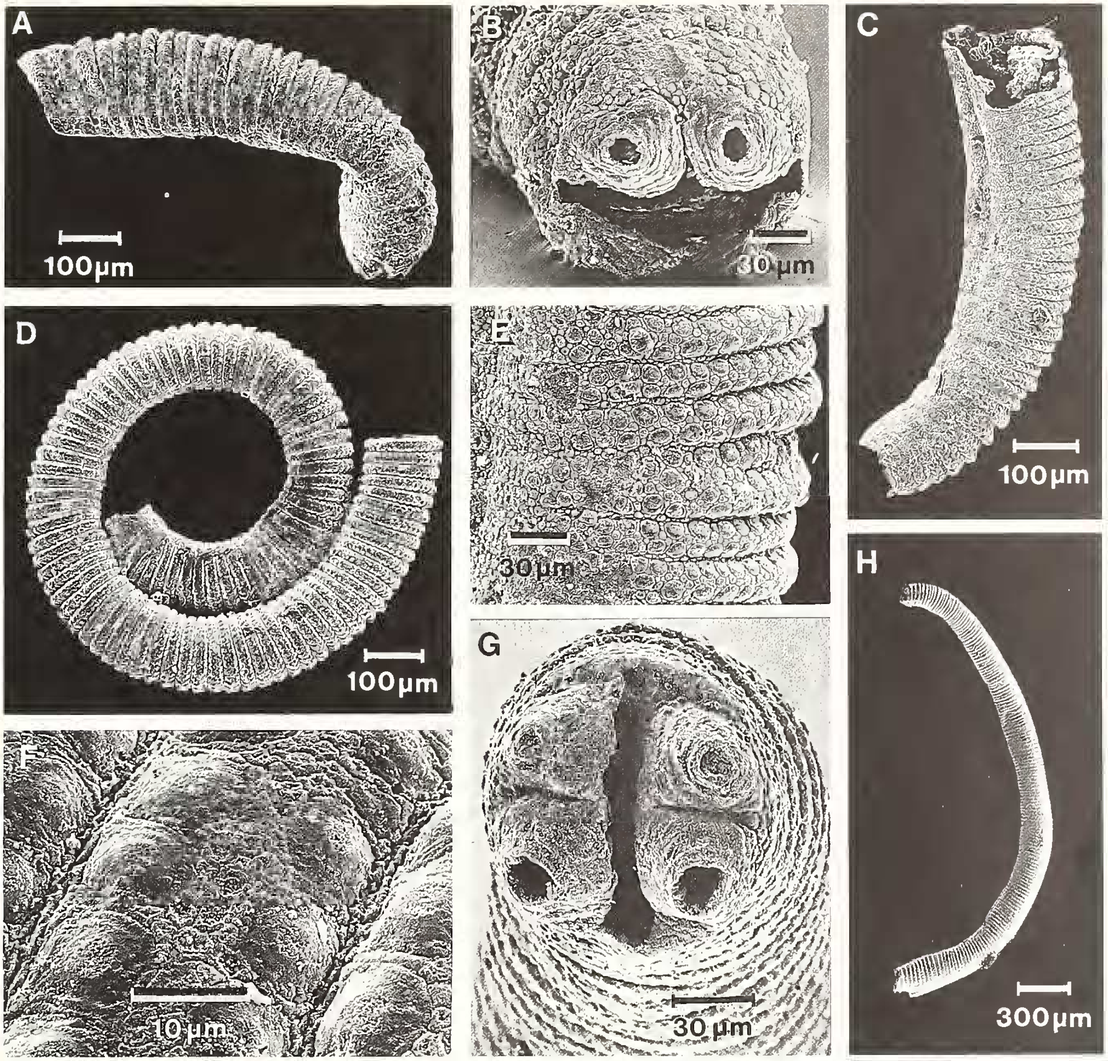
Remarks. Oral and aboral ends of fragmentary worms may be deduced from the annular inclination: the steep 'stoss' side is superimposed by the 'lee' side of the preceeding annulus. In this respect, the visible spines are assumed to point towards the aboral end.

This form differs from *Schistoscolex angustosquamatus* in the spine-like development of the median cone and in the convexity and inclination of annuli. Intercalations cannot be observed but the general pattern of ornamentation indicates that the species belongs to the same genus.

Schistoscolex umbilictus sp. nov.

Text-figs 11–12

Derivation of name. From *umbilicus*, Latin (navel) referring to the ornamentation of plates with elevated centre.

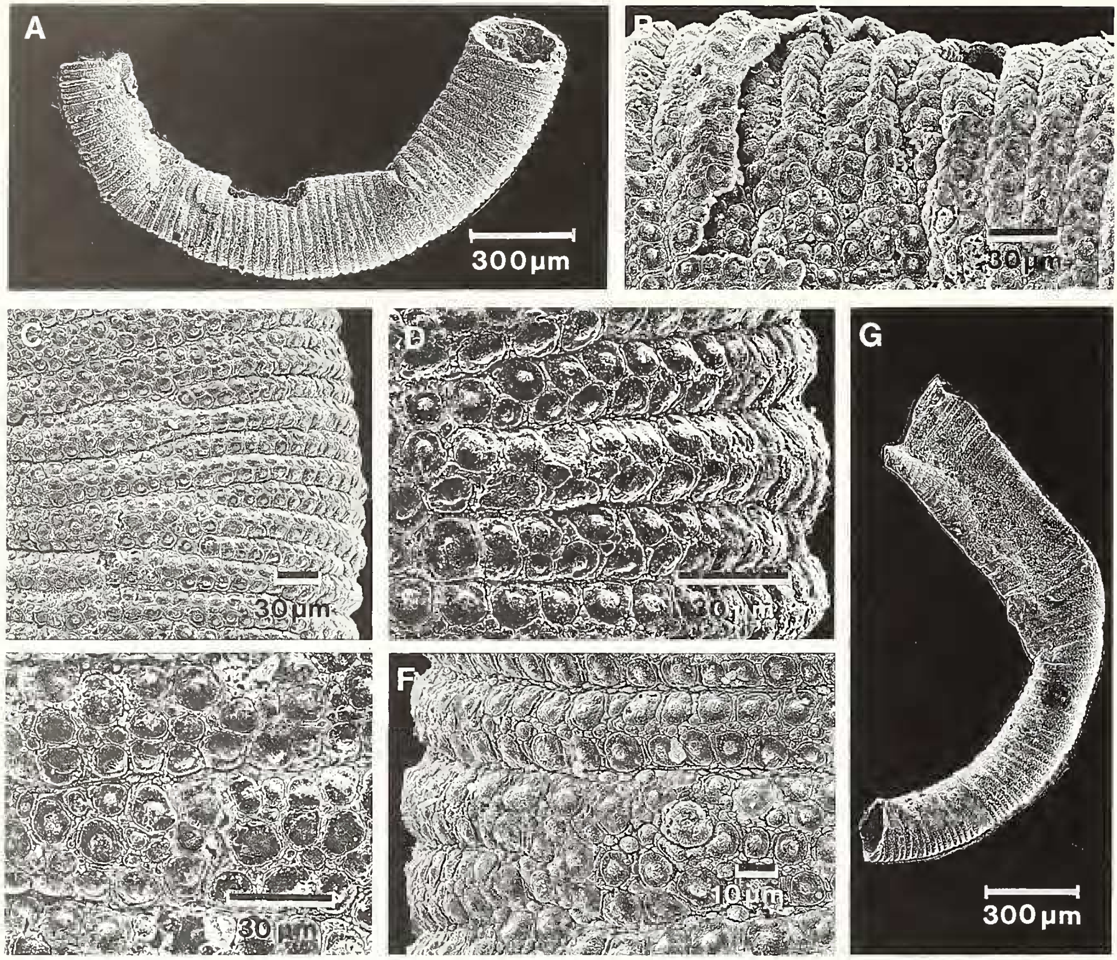


TEXT-FIG. 11. *Schistoscolex umbilicatus* gen. et sp. nov. A–B, CPC 23037 (sample 7335); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A, dorsolateral view, ×85. B, aboral view showing nipple-like appendages, ×265. C, E, CPC 23038 (sample 7335); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. C, ventrolateral view documenting ventral flattening of annulus profile, ×135. E, detail exposing narrow intercalations and dorsal furcation of ribs, ×265. D, F, CPC 23039 (sample 7324); Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. D, planispirally enrolled specimen, ×80. F, detail of strongly abraded surface ornamentation, ×1550. G–H, CPC 23040 (sample 7340); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. G, aboral view showing dorsoventral opening and two lateral pairs of nipples; the ventrally positioned nipples are larger than the dorsal ones, ×365. H, lateral view of slender, curved specimen, ×25.

Holotype. CPC 23041; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23037–23042.

Other material. 10 specimens.



TEXT-FIG. 12. *Schistoscolex umbilicatus* gen. et sp. nov. All specimens from 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A–D, CPC 23041 (sample 7335), holotype. A, oblique side view of terminally broken specimen, ×45. B, surface detail exposing underlying layer, ×100. C, detail with dorsal furcation of ribs, ×200. D, detail showing circular structure; this is regarded as a primary feature as the platelets are arranged concentrically around it, ×500. E–G, CPC 23042 (sample 7337). E, surface detail with irregular annulation, ×465. F, surface detail with furcation, ×550. G, general view of deformed specimen, ×40.

Diagnosis. Annulation narrow, partly furcated. Intercalations with elongate microplates. Annuli with two rows of closely spaced plates. Ornamentation of plates with one or two median nodes and smaller tubercles towards annulus border.

Description. Worms curved to planispirally enrolled; diameter of worm equal over entire length except for initial part and a slight increase towards the distal termination. Cross section circular. Aboral end with four, slightly outwardly-directed nipples. According to the curvature of the worm they are arranged as a smaller dorsal and a larger ventral pair (Text-fig. 12G). An elongate opening between these pairs results from the inwardly folded cuticle (Text-fig. 17A–C).

Annulation irregular in width. Dorsal bi- or trifurcation with an increased number of rows of plates observed (e.g. Text-fig. 12C, F). Furcated ribs highly convex and narrowly folded dorsally, the ventral side being more flattened. Intercalations very narrow and consisting of elongate platelets that are irregular in shape and arrangement.

Ornamentation of annuli with two rows of comparatively large plates. Both rows consist of similar plates that are in direct contact with each other or leave only a narrow interspace. They are rounded with irregular margins and characterized by one or two median cones. Some comarginal tubercles may be developed towards the annulus borders. Both rows are separated by a mosaic pattern of platelets. On the ventral face the plates are more irregularly arranged than on the dorsal face (Text-fig. 12F).

Platelets irregular in shape, varying from almost hexagonal to elongate or completely irregular. A nodular sculpture may be present. Elongate platelets occur predominantly between the plates of a single row. Plates:platelets ratio about 7:3.

Schistoscolex sp. indet.

Text-fig. 13

Illustrated material. CPC 23043–23045; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Other material. 1 specimen.

Description. Gently curved worms with circular cross-section. Annuli slightly variable in width on the dorsal side; ventral width much more irregular and dependent on the degree of curvature. Intercalations sometimes overlapped on the ventral side (Text-fig. 13E). Ornamentation of annuli with irregularly arranged plates. Plates with irregularly rounded outline and central elevation. Interspaces filled with small, irregularly polygonal platelets.

Ventral side of worms characterized by more-or-less paired nipples on each third or fourth annulus (Text-fig. 13C–E). The nipples are outwardly directed. Smaller nipples indicated close to larger nipples on the same or on an adjacent annulus. Around the nipples, the cuticle is folded and the annulus is widened.

Remarks. Structures which may represent the broken bases of tubules (compare also Text-figs 5E–F and 8E–F) appear to be randomly distributed over the entire surface. They are surrounded by concentrically arranged tiny plates. These tubules are similar to those described in the praipulid *Halicryptus spinulosus* by Oeschger and Janssen (1991). Plates:platelets ratio about 1:2.

Genus SHERGOLDISCOLEX gen. nov.

Type species. Shergoldiscolex nodosus sp. nov.

Derivation of name. In honour of Dr John H. Shergold, Bureau of Mineral Resources, Canberra, Australia.

Diagnosis. Annulation moderately broad, intercalations narrow with oval, nodular microplates. Annuli with two rows of highly ornamented plates. Central annular zone narrow to medium broad.

Shergoldiscolex nodosus sp. nov.

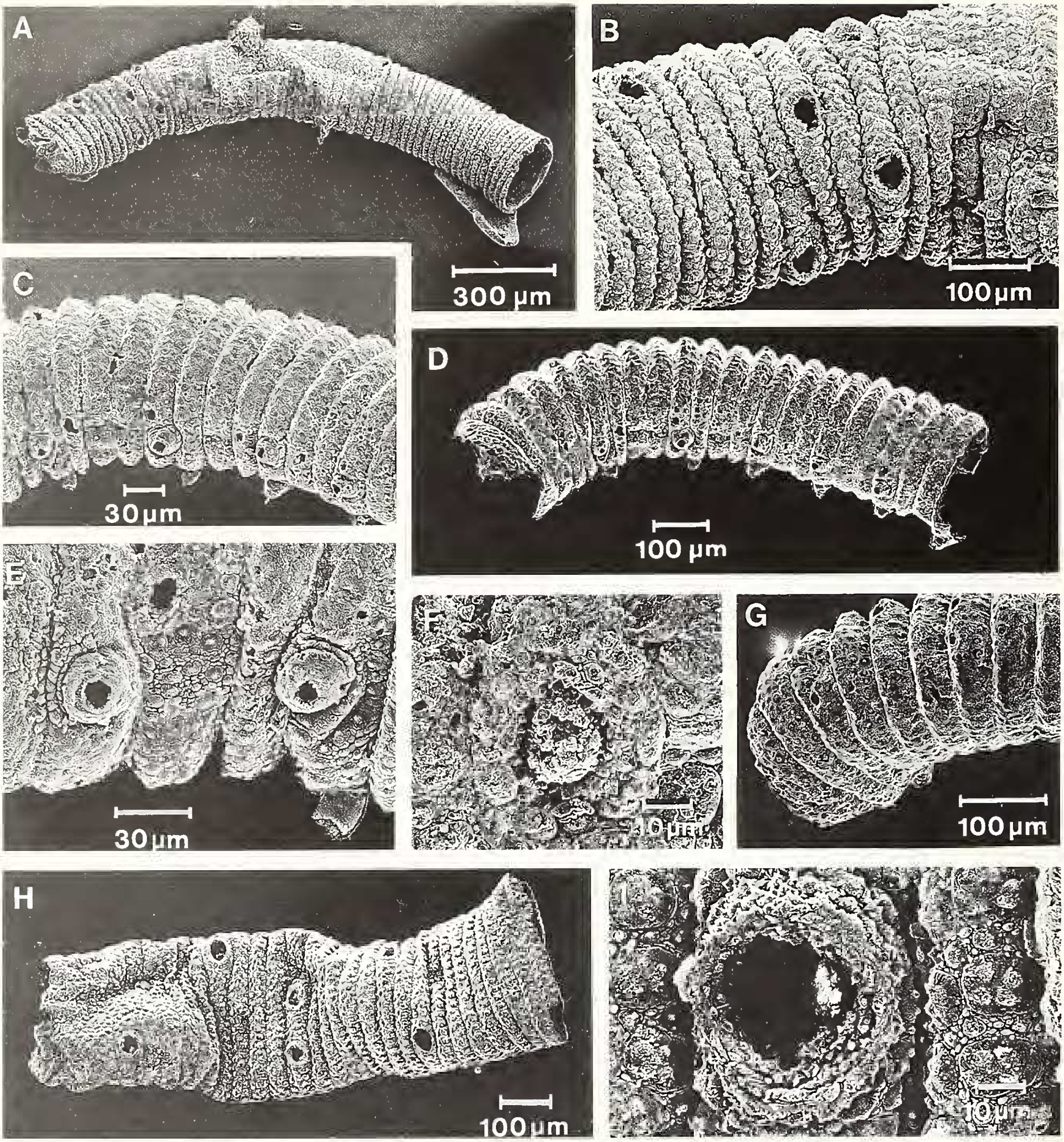
Text-fig. 14G–M

Derivation of name. From *nodosus*, Latin (full of nodes), referring to the extremely rich ornamentation of plates.

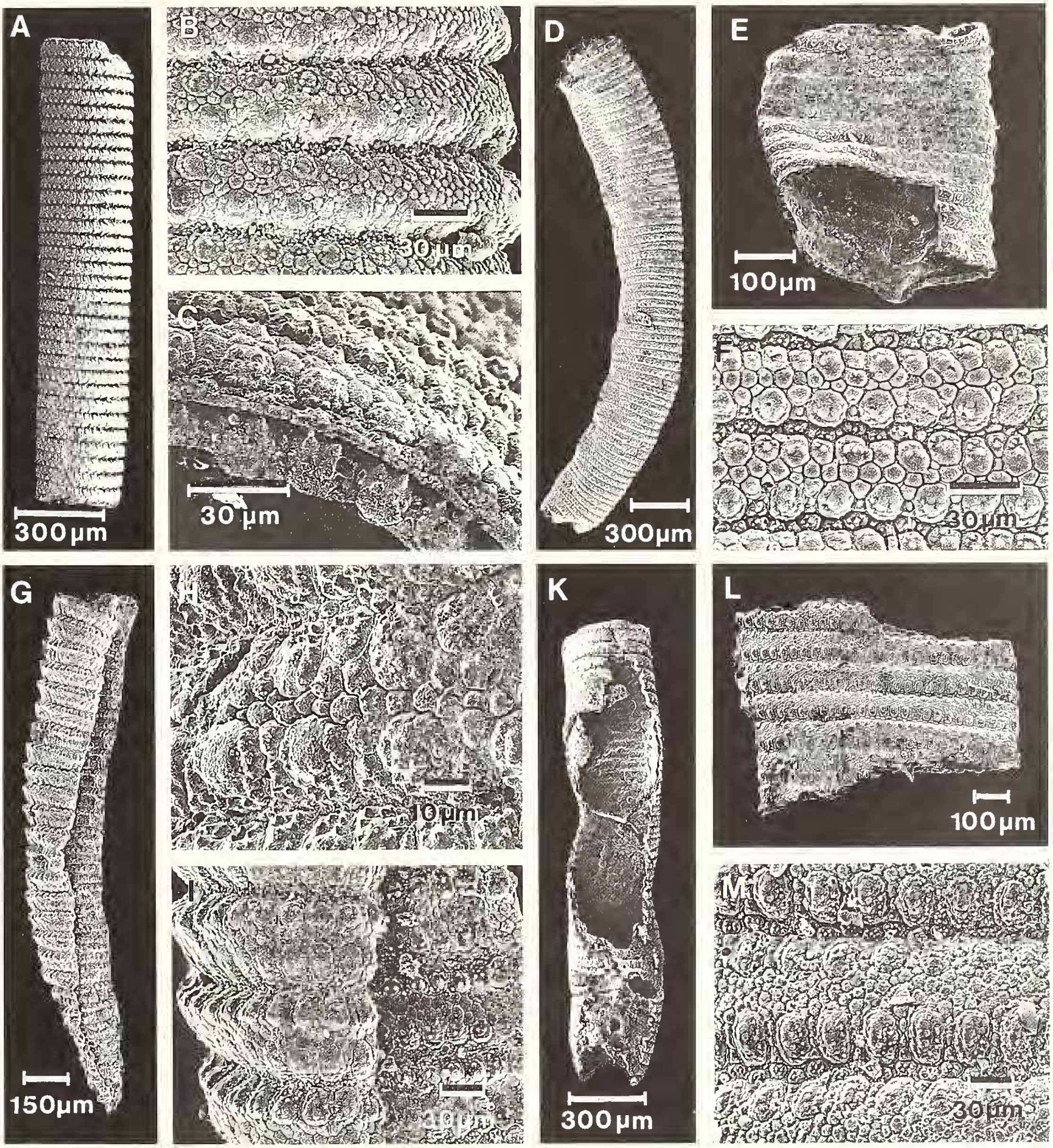
Holotype. CPC 23051; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. CPC 23049–23051.

Other material. 4 specimens.



TEXT-FIG. 13. *Schistoscolex* sp. indet. All specimens from 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A–B, CPC 23043 (sample 7338). A, ventrolateral view of terminally broken specimen; annuli with irregularly-distributed openings; width of annuli increased at these openings, × 45. B, detail of same specimen, × 110. C–G, CPC 23044 (sample 7338). C, ventrolateral view with parallel rows of nipple-like appendages; nipples are positioned on every third to fourth rib; width of rib increased around nipple, × 185. D, general view of specimen, × 75. E, detail of ventral side with irregular annulation and insertion of nipples, × 335. F, surface detail with proximal part of tubule; note circular arrangement of platelets around this structure, × 650. G, surface detail of dorsal side with irregularly distributed openings, × 120. H–I, CPC 23045 (sample 7336). H, general view of fragmentary specimen, × 70. I, detail of surface with basis of tubule, × 700.



TEXT-FIG. 14. *Shergoldiscolex* gen. nov. All specimens from 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A–F, *Shergoldiscolex polygonatus* sp. nov. A, C, CPC 23046 (sample 7339). A, general view of straight specimen, ×40. C, view onto oral side with another, underlying, completely armoured cuticle that could represent a stage shortly before moulting, ×470. B, D, CPC 23047 (sample 7338). B, surface detail, ×265. D, lateral view of curved specimen; the variable depressions on the outer surface are of a secondary nature, ×25. E–F, CPC 23048 (sample 7335), holotype. E, lateral view of compressed, fragmentary specimen, ×85. F, surface detail showing intercalations between the annuli, ×335. G–M, *Shergoldiscolex nodosus* sp. nov. G, I, CPC 23049 (sample 7336). G, oblique lateral view of inwardly-folded specimen, ×45. I, surface detail showing inclination of annuli towards aboral end, ×200. H, K, CPC 23050 (sample 7335). H, surface detail with rich ornamentation, ×700. K, general view of fragmentary specimen; the inner side reflects the outer ribbing, ×35. L–M, CPC 23051 (sample 7336), holotype. L, large, compressed fragment, ×50. M, detail of surface with intercalations, ×200.

Diagnosis. Annulation variably broad, with two rows of large, highly ornamented plates. Within a single annulus, one row has larger plates than the opposite row. Ornamentation of plates with elevated centre surrounded by smaller tubercles. Triangular microplates between plates in one row, polygonal platelets in central annular zone.

Description. Fragmentary specimens without oral and aboral ends. Annulation may be somewhat variable in width. Intercalations narrow with a single row of irregularly oval, nodular microplates.

Contracted annuli with asymmetrical, roof-like relief (i.e. with a triangular cross-section). One face consists of a row of plates, the other face comprises the plates plus the central annular zone. Annuli ornamented by two, non-identical rows of plates that are in close contact with the microplates of the intercalations. Outline of plates circular to irregularly polygonal. Centre elevated, and with four to six nodes surrounded by tubercles that form a double or triple row at the short axis. In the opposite row the plates may lack a large central elevation; instead, many small nodes are developed. In general, the plates are not bilaterally symmetrical. There is a high variability in fine details. Between plates, subtriangular microplates with nodular surface are intercalated.

Platelets with polygonal outline and smooth margins, highly variable in size. Platelets more elongate between plates than in the centre of annulus. Surface partly nodular, in particular between the plates of a single row. Plates:platelets ratio about 2:1.

Shergoldiscolex polygonatus sp. nov.

Text-fig. 14A–F

Derivation of name. From *polygonatus*, Latin, referring to the outer shape of sclerites.

Holotype. CPC 23048; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Material. CPC 23046–23048.

Diagnosis. General characters as for the genus. Plates irregularly polygonal with central elevation of partly fused nodes. Smaller tubercles developed towards annulus borders. Polygonal platelets of central annular zone fairly large.

Description. Worm fragments with flat annular relief. Intercalations present. Plates within an annulus crudely rounded to irregularly polygonal and rather variable in size. Centre of plates highly convex with one to several, partly fused nodes. Outer circle of tubercles mostly incomplete and best developed towards the annulus border. Platelets forming a mosaic pattern of polygons; size of platelets relatively large, sometimes approaching the size of a small plate that is distinct only by its ornamentation. Plates:platelets ratio about 2:3.

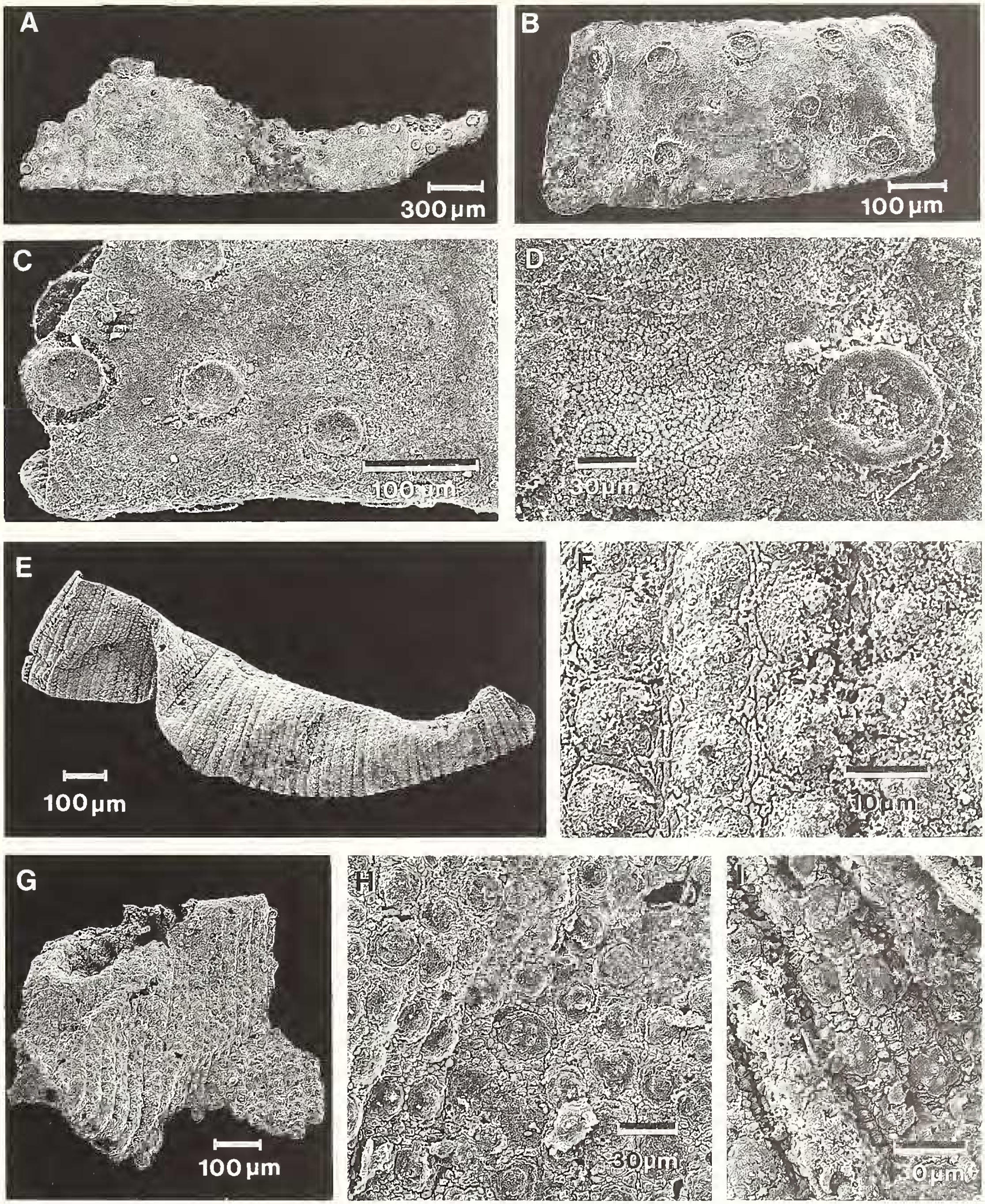
Remarks. The specimen illustrated in Text-figure 14C is composed of two overlying armoured cuticles. The upper armour shows traces of abrasion, whereas the armour beneath has plates with still pointed nodes or cones. The particular specimen is regarded as possible evidence for moulting of palaeoscolecids.

Genus THORACOSCOLEX gen. nov.

Type species. Thoracoscolex armatus sp. nov.

Derivation of name. From *thorax*, Greek (armour), referring to the armour of the cuticle.

Diagnosis. Annulation narrow, intercalations small. Annuli with two rows of densely-packed, circular plates. Ornamentation of plates with two to five central nodes.



TEXT-FIG. 15. A–D, *Euryscolex paternarius* gen. et sp. nov.; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A, C, CPC 23052 (sample 7339). A, general view of fragment with extremely flat relief, × 30. C, detail showing plates with exfoliated, ribbed girdle and concave, radially ribbed upper sides, × 175. B, D, CPC 23053 (sample 7336), holotype. B, general view of large fragment, × 85. D, surface detail showing mosaic pattern of platelets, × 315. E–I, *Thoracoscolex armatus* gen. et sp. nov. E–F, CPC 23054 (sample 7324), holotype; Mt Murray, late Templetonian, *Triplagnostus gibbus* Zone. E, general view of deformed specimen, × 65. F, surface detail of tight armour with small, elongate platelets between rows of ribs, × 1300. G–H, CPC 23055 (sample 6958). G, general view of fragment, × 70. H, detail of surface, × 285. I, CPC 23056 (sample 7339); detail of surface showing ornamentation of platelets, × 365.

Thoracoscolex armatus sp. nov.

Text-fig. 15E–I

Derivation of name. From *arma*, Latin (armour).

Holotype. CPC 23054; from 1 km north of Mt Murray, Duchess, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Illustrated material. 23054–23056.

Other material. 2 specimens.

Diagnosis. As for the genus.

Description. Large, fragmentary worms; oral and aboral ends not preserved. Intercalations between annuli rather narrow and formed by a single row of irregular platelets (Text-fig. 15I). Sometimes intercalations are in part widened slightly by a second row of even smaller platelets.

Annuli rather narrow and moderately convex. Ornamentation consisting of two rows of irregularly alternating plates. Plates with subcircular outline and undulating or jagged marginal rims. Surface moderately convex with two to five nodes; the most frequent pattern displays four nodes. Outline and ornament highly variable with regard to number and position of nodes. Platelets rather variable from rope-like to irregularly rounded, the latter with highly convex upper side and partly jagged margins. Size difference to plates considerable. Plates:platelets ratio about 9:1.

Palaeoscolecida gen. indet. cf. *Hadimopanella apicata* Wrona, 1982

Text-fig. 16G–H

cf. 1982 *Hadimopanella apicata* Wrona, p. 11, pls 1–4.
cf. 1984 *Hadimopanella apicata* Wrona; Peel and Larsen, p. 93, figs 2–5.
cf. 1987 *Hadimopanella apicata* Wrona; Hinz, p. 80, pl. 4, fig. 6.
cf. 1988 *Hadimopanella apicata* Wrona; Bendix-Almgreen and Peel, pp. 85–91, figs 3–7.

Material. Figured specimen, CPC 23061; from Rogers Ridge, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

Description. Isolated, thick, subcircular plate with pronounced central cone that is steeply emerging. Outer rim of plate slightly scalloped; the broad periphery is marked by comparably coarse vertical structures (Text-fig. 16H).

Remarks. This specimen is considered to be related to *Hadimopanella apicata* based on the very distinct feature of a strongly developed central cone. In our specimen the steep cone has almost parallel sides, in contrast to the approximately triangular profile of the taxa referred to in the synonymy.

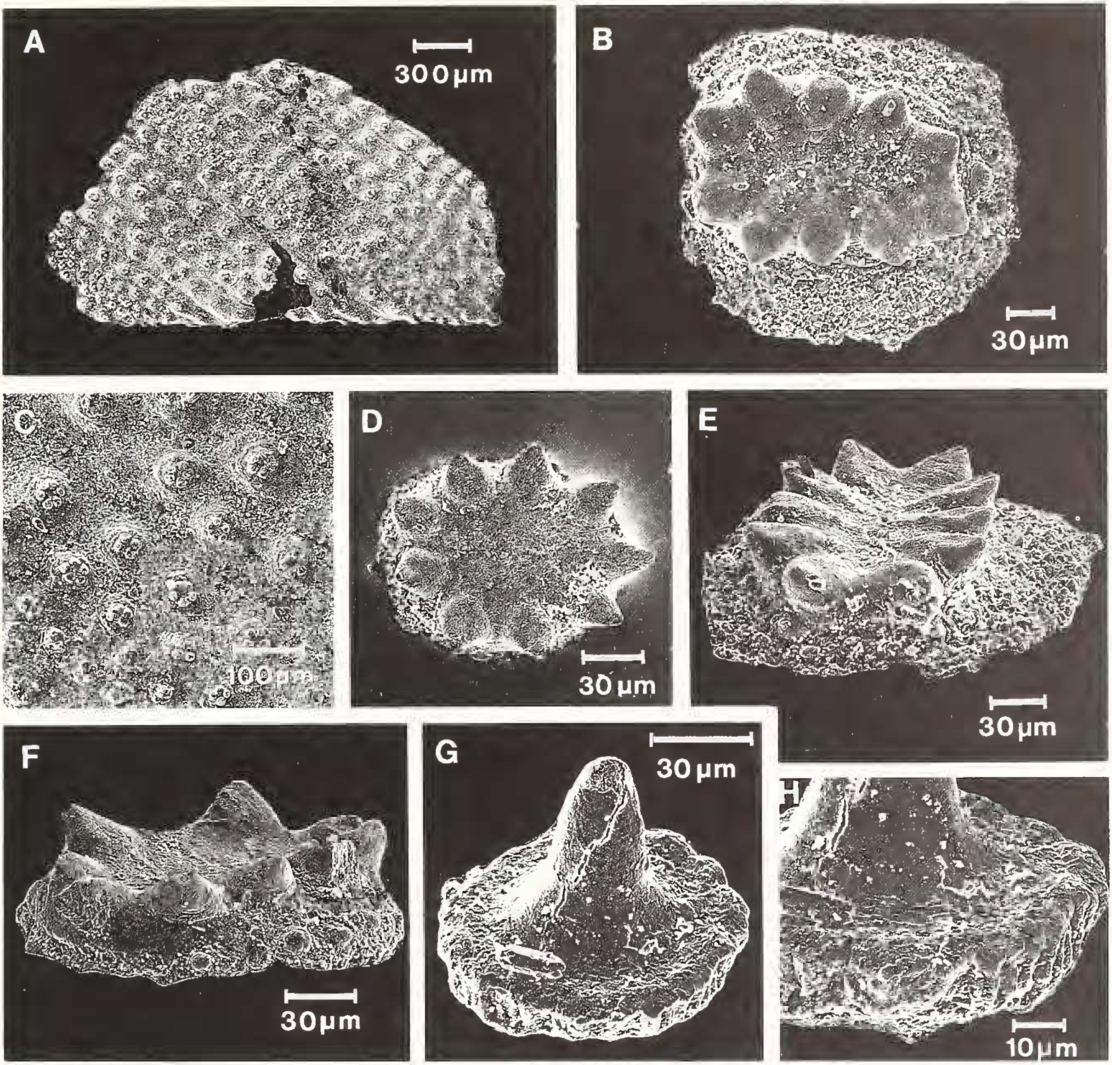
Palaeoscolecida gen. indet. sp. A

Text-fig. 16B, D–F

Illustrated material. CPC 23058–23060; Rogers Ridge, Queensland; *Triplagnostus gibbus* Zone, Middle Cambrian.

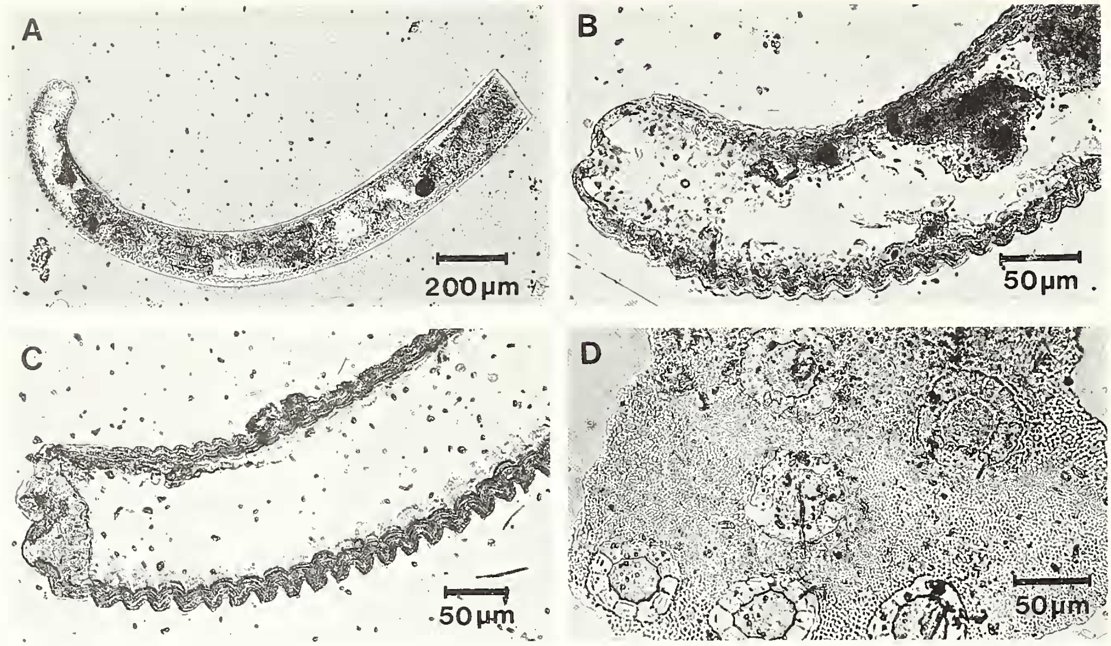
Other material. 147 specimens.

Description. Sclerites of variably oval outline. Upper surface smooth with marginally distributed, relatively large cones. Cones with outwardly-directed tips and rather flat profiles. Upper surface of cones frequently with



TEXT-FIG. 16 A, C, *Pantoioscolex oleschinskii* gen. et sp. nov., CPC 23057 (sample 7331), holotype; 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone. A, general view of fragment, ×25. C, detail of surface, ×95. B, D–F, Gen. indet. sp. A, Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone. B, E, CPC 23058 (sample 7283). B, view from above, ×215. E, oblique lateral view; note enlarged basal portion with minute cones, ×250. D, CPC 23059 (sample 7282); oblique view from above, ×285. F, CPC 23060 (sample 7283); oblique lateral view; note tiny marginal cones on basal portion, ×315. G–H, Palaeoscolecida gen. indet. cf. *Hadimopanella apicata* Wrona, CPC 23061 (sample 7283); Rogers Ridge, late Templetonian, *Triplagnostus gibbus* Zone. G, oblique lateral view, ×450. H, surface detail of marginal rim, ×235.

shallow depression (Text-fig. 16E). Cones continue towards centre of sclerite in faint, alternating ridges (Text-fig. 16F). Lower surface probably fibrous, but preservation prevents precise statements. Some specimens show additional, much smaller cones along with the lower marginal rim (Text-fig. 16F). A single sclerite even has a much expanded lower side with several rows of minute cones interbedded (Text-fig. 16B, E).



TEXT-FIG. 17. Palaeoscolecida gen. et sp. indet. A–B, CPC 23062 (sample 7503); drilling Duchess 18, late Templetonian, *Triplagnostus gibbus* Zone. A, longitudinal section showing multilamellar wall structure and aboral invagination, ×45. B, detail of aboral portion, ×210. C, CPC 23063 (sample 7340); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone; longitudinal section; detail of aboral portion with invagination; note different annular relief of dorsal and ventral sides, ×160. D, CPC 23064 (sample 7331); 1 km north of Mt Murray (= D640), late Templetonian, *Triplagnostus gibbus* Zone; section through cuticle parallel to surface, showing plates with broad marginal brim which is usually embedded in tissue, ×200.

INTERNAL STRUCTURE AND GROWTH

Palaeoscolecida are soft-bodied fossils that have their cuticle reinforced by an armour of sclerotized plates and platelets. The cuticle itself is stratified (Text-fig. 17A–C), up to seven layers having been observed. Traces of an underlying secretory epidermis and muscles have not been identified. However, a variable degree of bodily contraction (i.e. steep to flat annuli) points to muscular activity. Depending on the degree of contraction, the annulation is visible on both outer and inner sides of the cuticle, but it is not considered to reflect segmentation or metamerism.

The plates are most probably primarily mineralized; previous detailed investigations by Bengtson (1977), Wrona (1982, 1987), Dzik (1986) and Bendix-Almgreen and Peel (1988) have revealed a dense, apparently non-lamellar capping and a fibrous core. The fibrils probably facilitated attachment to the cuticle. The upper surface of plates visible on a preserved cuticle is much smaller than their basal diameter. The plates are anchored along a broad rim marked by radial structures. On isolated specimens of *Hadimopanella collaris* Märss, 1988 a similar marginal structure can be observed, as can be seen in a thin section of a specimen parallel to the outer surface (Text-fig. 17D). Partly exfoliated surfaces of different taxa reveal a matrix for anchoring plates and adjacent platelets.

The plates achieve their definite ornament only in the uppermost layer. Further inward, the ornament simplifies and the plates decrease in size until they cannot be distinguished from platelets. The armoured cuticle is more-or-less equally thick over the entire length of a worm; thickness only decreases aborally at the paired nipples. From a slit-like aboral opening the cuticle is invaginated to form a blind sac (Text-fig. 17B–C). The outer surface of the aboral region appears either smooth or ornamented with relatively small, more-or-less equally developed platelets, independent of the general annular ornament of the worm.

Palaeoscolecida are assumed to have grown by moulting. This assumption is strengthened by the armour of their cuticle which permitted only limited elasticity. Furthermore, within a single taxon, there are remarkable differences in width with specimens ranging from less than 400 μm to more than 800 μm, or from about 700 μm to 1500 μm. The specimen illustrated in Text-figure 15A–C is assumed to document the development of a young stage. The young stage has the same ornament and arrangement of plates as the older stage, but the interspace between the single plates is relatively smaller. The new cuticle is even a little folded because of the increased diameter. Obviously the platelets are not fully developed. Length is considered to have increased proportionally by the same procedure: plates of an annulus are more closely-spaced until the development of platelets sets them apart.

Due to lack of suitable material, the number of moult stages remains unclear. Furthermore, it is unknown whether this number varies between individual taxa. It is possible that forms with large central annular areas would have needed fewer stages than those with closely-spaced plates because in the former the annuli had little opportunity to expand with each moult.

VARIABILITY

First of all, we have to distinguish between variability within a single taxon and variable characters on the same individual. Intraspecific variation affects almost all available characters, such as the widths of the annuli and central annular zone (e.g. Text-fig. 8A, G–K), and size and ornamentation of plates (e.g. Text-fig. 15B, H).

In the species descriptions the plates:platelets ratio is added as a further aid for the characterization of a taxon. However, with regard to variability it is not systematically significant, even if the degree of variation differs distinctly between the various taxa.

More important for the present material is the variability of features on the same animal. This is shown by: (1) an irregular annulation (Text-fig. 10F); (2) an irregular mode of furcation (Text-fig. 12C) which results in differentiation of ornament between dorsal and ventral sides (Text-fig. 11E); (3) the size difference between plates of a single row (Text-fig. 9B); and (4) a generally variable surface ornamentation within certain limits. *Austroscolex* (Text-fig. 5) and *Rhomboscolex* (Text-fig. 9) are distinguished by their overall appearance, but their individual plates show similarities. The same applies to isolated plates of *Murrayscolex* and *Shergoldiscolex* which are separated on the basis of presence or absence of intercalations. Eventually, different forms could prove to be only morphotypes of a single taxon, or the same types of plates could have developed convergently. These observations indicate that some isolated plates may be taxonomically unassignable.

FUNCTIONAL MORPHOLOGY

The interpretation of isolated plates as dermal sclerites first given by Bengtson (1977) is confirmed by findings of integuments of Palaeoscolecida.

The armoured cuticle was not as stiff as in other tubular fossils such as serpulids, styliolinids, tentaculites etc. It consists of individual rows of plates with the interspace between filled with tiny polygonal platelets. They do not form a complete mineralized cover but rather lie in soft tissue that permits a certain elasticity. The plates and platelets are completely mineralized components. The organic matter that previously filled the interspaces between these components is now left as distinct gaps (Text-fig. 8K).

The worms are not assumed to have had great mobility. In particular, enrolled specimens with bifurcated ribs at the dorsal side and insertion of rows of platelets point to quite a stable life attitude with limited ability for dilatation and shrinkage only. Therefore, locomotion by contraction and dilatation as well as snake-like, lateral movements are unlikely to have occurred. The function of the aboral invagination is unclear. It might have enabled the four appendages to perform movements such as straddling.

Wear of nodes on the upper surface of plates has been previously observed on isolated plates (Bengtson 1977; van den Boogaard 1983). Functional wear can be distinguished from secondary abrasion during sedimentation by studying the outer rim of the plates which was originally embedded in integument and thus sheltered. Plates with eroded margins point to transportation which has been proved for the high energy environments of the Duchess area.

ECOLOGY

Little is known about the mode of life of Palaeoscolecida. Gedik (1981) assumed that they were nektonic, whereas Runnegar (1982) presumed a burrowing habit. Our material, which mostly comes from Mt Murray in the Duchess Embayment, is apparently current-washed so that the original ecological context has been lost. The material presents such a wide range of shapes and ornamentations that the animals are assumed to have occupied different ecological niches rather than lived in one place.

Some of the plates show abrasion which points to living on or in a much coarser sediment than the calcareous mud in which they were collected. Other taxa (e.g. *Schistoscolex*) with long, non-abraded spines probably preferred a different environment. Also the fact that the worms have been discovered in various attitudes (from slightly curved to planispirally enrolled) supports the assumption of different environments.

Boogaard (1983, p. 334) demonstrated the wide variation of sample productivity in successive beds of various stratigraphical sections and concluded that it is not due to diagenetic or later processes, but the result of varying biological and/or sedimentological conditions.

PHYLETIC RELATIONSHIPS

Palaeoscolecida have been tentatively referred to the phylum Annelida because of their annular outline that was interpreted as segmentation, and evidence of bodily contraction and relaxation. However, the preserved annular cuticle seems to us insufficient to indicate a relationship with Annelida. The main characteristic of this phylum is metamerism, i.e. the repetition of identical internal structures such as coelomic spaces, nerves, etc. The probable occurrence of chetae (Whittard 1953) in Palaeoscolecida was not confirmed in subsequent studies (see the discussions of Whittard's paper by Thomas (*in* Whittard 1953) and Conway Morris and Robison (1986)) or in the well-preserved material studied herein. This clearly demonstrates that the 'papillae' are in fact nodes. In some cases (e.g. *Hadimopanella coronata* Boogaard, 1989) they may even be developed as spines. In our opinion, an assignment to annelids is unlikely.

Another group of worms which are known back to the Early Cambrian are the Priapulida. They are characterized by an eversible proboscis.

The occurrence of tubules, which are irregularly distributed over the whole surface, and the presence of plates may suggest a relationship with the Aschelminthes at least in a wider sense (R. M. Kristensen pers. comm.). Similar tubules are, for example, present in all developmental stages of priapulids (D. Walossek pers. comm.).

COMPARISONS

From Lower Palaeozoic sediments, mainly Cambrian, a number of different genera are known that have been assigned to Onychophora, Priapulida and Annelida. These forms are briefly discussed and compared with our palaeoscolecidan material.

The type species of *Palaeoscolex*, *P. piscatorum* Whittard, 1953, comprises relatively large specimens which are usually flattened on shale. The body shows distinct annulation and most of it is also decorated with plates, but the precise ornament of the plates is indeterminable. This is due particularly to the fact that one of the inner layers is usually exposed. In splitting the shales, at least part of the outer surface adheres to the rock and, as is seen in our material, the ornament becomes increasingly indistinct towards the inner side. The ornamentation, however, is a diagnostic character, together with the arrangement of plates and the development of platelets. Therefore, none of the new Australian taxa could be assigned to *Palaeoscolex*. *Palaeoscolex piscatorum* displays a structure similar to an inner layer of *Corallioscolex*.

Protoscolex Ulrich, 1878, from the Upper Ordovician, probably belongs to the Palaeoscolecida. As the form is not represented in our material, we have not studied it in detail.

Cricocosmia Hou and Sun, 1988, from the Lower Cambrian of South China, is an annulated worm with one to two pairs of highly convex plates on each annulus. This is different to the ornamentation of Palaeoscolecida and also different to Priapulida which have a narrowly annulated but unornamented middle part. Further, a proboscis is not recognizable on *Cricocosmia* and its reference to Priapulida is doubtful.

Maotianshania Sun and Hou, 1987, from the Lower Cambrian of Yunnan Province is likely to belong to the priapulids. Its blunt aboral end bears a spine, and orally it terminates in a spiny proboscis. The specimens are compressed and preserved on the bedding surfaces of shale and mud.

VALUE FOR STRATIGRAPHY

Palaeoscolecidan remains obviously are much more widespread and common than is evident from the literature. This is shown by the fact that hadimopanellids since their first description some 14 years ago have been reported from many localities by various authors. They may form a large component of the sediment. Whittard (1953) recorded up to 30,000 plates on a single individual. Their assumed benthic mode of life suggests restriction to certain facies.

Märss (1988) believed that the established species of *Hadimopanella* may be of some help for stratigraphical purposes, although Palaeoscolecida, as a Class, are long-ranging. Gedik (1989) described the stratigraphical distributions of *Hadimopanella* species in the western Taurids, Turkey, and suggested a biostratigraphical zonation within the Lower, Middle and Upper Cambrian. However, his diagram shows considerable ambiguity about the lower and upper ranges of the individual species. Furthermore, as the limestones and dolomites of his sections are quite variable in lithology, the occurrence and disappearance of Palaeoscolecida may be facies controlled.

The stratigraphical application of isolated plates is hampered because the same types of plates may occur in different genera. What would have been described as different species if not genera, may turn out to be mere morphotypes.

It is expected that the various taxa will have different potentials as index fossils; some may be long-ranging, while others may be restricted to short-time intervals. This can be determined only empirically, and much more information is needed before Palaeoscolecida can be confidentially applied in correlation. Even 'species' may not be restricted to zones. Common form-species have already turned out to be long-ranging. *Hadimopanella oezguli* Gedik, 1977, was originally described from the Upper Cambrian of the Middle Taurus, Turkey but is also present in the Middle Cambrian of Australia (herein) and South Kirgizia (Märss 1988), as well as in Cambro-Ordovician boundary beds in Estonia (*Hadimopanella collaris* Märss, 1988, in part). Again, *Milaculum ruttneri* Müller was originally described from the Upper Cambrian of Iran and has been subsequently described as *Plasmuscolex nero* and *Plasmuscolex klabavensis* Kraft and Mergl, 1989 from the Arenig of Bohemia.

Until the present study, only flattened specimens had been reported from shales. In this type of preservation the plates and platelets of the surface commonly are not well-preserved. Accordingly, critical details in ornamentation could not be observed. The fair variety in morphology of these plates permits the possibility of investigating their potential as index fossils. But the standard has to be established at a section where the specimens are not current-washed, unlike our material.

Acknowledgements. The material was collected during a joint project between the Bureau of Mineral Resources, Canberra and the University of Bonn in order to investigate the microfauna of the Middle Cambrian Georgina Basin phosphorites. We would like to thank John Shergold (Canberra) for logistics and permission to reproduce Text-figures 1 and 2, R. Below (Utrecht) and D. Walossek (Bonn) for sampling, and Mrs A. Gossmann, Mrs D. Kranz and Mr G. Oleschinski for valuable technical help. Critical reading by S. Conway Morris (Cambridge) is appreciated. The project has been kindly supported by the Deutsche Forschungsgemeinschaft.

REFERENCES

BATHER, F. A. 1920. *Protoscolex latus*, a new "worm" from Ludlow Beds. *Annals and Magazine of Natural History*, (9), **5**, 124–132.

BENDIX-ALMGREEN, S. E. and PEEL, J. S. 1988. *Hadimopanella* from the Lower Cambrian of north Greenland: structure and affinities. *Bulletin of the Geological Society of Denmark*, **37**, 83–103.

BENGTSON, S. 1977. Early Cambrian button-shaped phosphatic microfossils from the Siberian Platform. *Palaeontology*, **20**, 751–762.

—— and CONWAY MORRIS, S. 1984. A comparative study of Lower Cambrian *Halkieria* and Middle Cambrian *Wiwaxia*. *Lethaia*, **17**, 307–329.

BOOGAARD, M. VAN DEN 1983. The occurrence of *Hadimopanella oezgueli* Gedik in the Lancara Formation in NW Spain. *Proceedings of the Koninklijke Akademie van Wetenschappen, Series B*, **86**, 331–341.

—— 1988. Some data on *Milaculum* Müller, 1973. *Scripta Geologica*, **88**, 1–25.

—— 1989*a*. A problematic microfossil, *Hadimopanella*? *coronata* sp. nov., from the Ordovician of Estonia. *Rijksmuseum van Geologie en Mineralogie, Series B*, **92**, 179–190.

—— 1989*b*. Isolated tubercles of some Palaeoscolecida. *Scripta Geologica*, **90**, 1–12.

CHEN JUN-YUAN, HOU XIAN-GUANG and LU HAO-ZHI 1989. [Early Cambrian netted scale-bearing worm-like sea animal]. *Acta Palaeontologica Sinica*, **28**, 1–16, pls 1–4. [In Chinese with English summary].

——, BERGSTRÖM, J., LINDSTRÖM, M. and HOU XIAN-GUANG 1991. Fossilized soft-bodied fauna. *National Geographic Research and Exploration* **7**, 8–19.

CONWAY MORRIS, S., PICKERILL, R. K. and HARLAND, T. L. 1982. A possible annelid from the Trenton Limestone (Ordovician) of Quebec, with a review of fossil oligochaetes and other annulate worms. *Canadian Journal of Earth Sciences*, **19**, 2150–2157.

—— and ROBISON, R. A. 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *University of Kansas Paleontological Contributions*, **9**, (Paper 117), 1–22.

COOK, P. J. and SHERGOLD, J. H. 1980. *Proterozoic-Cambrian phosphorites. Project 156.* Canberra Publishing and Printing Co., Canberra, xi + 106 pp.

DZIK, J. 1986. Chordate affinity of the conodonts. 240–254. *In* HOFFMANN, A. and NITECKI, M. H. (eds). Problematic fossil taxa. *Oxford Monographs on Geology and Geophysics*, **5**, 267 pp.

ETHINGTON, R. and CLARK, D. L. 1965. Lower Ordovician conodonts and other microfossils from the Columbia Ice Fields Section, Alberta, Canada. *Brigham Young University Geological Studies*, **12**, 185–205.

GAZDZICKI, A. and WRONA, R. 1986. Polskie Badania Paleontologiczne W Antarkyce Zachodnij. *Przeglad Geologiczny*, **11**, 609–617.

GEDIK, I. 1977. Conodont stratigraphy in the Middle Taurus. *Bulletin of the Geological Society of Turkey*, **20**, 35–48.

—— 1981. *Hadimopanella* Gedik, 1977 nin stratigrafik dagilimi ve mikroyapisi konusunda bazi gözlemler. *Karadeniz Teknik Üniversitesi Yer Bilimleri Dergisi, Jeoloji*, **1**, 159–163.

—— 1989. Hadimopanellid biostratigraphy in the Cambrian of the Western Taurids: A new biostratigraphic tool in the subdivision of Cambrian System. *Geological Bulletin of Turkey*, **32**, 65–77.

GLAESSNER, M. F. 1979. Lower Cambrian Crustacea and annelid worms from Kangaroo Island, South Australia. *Alcheringa*, **3**, 21–31.

HINZ, I. 1987. The Lower Cambrian microfauna of Comley and Rushton, Shropshire/England. *Palaeontographica, Abteilung A*, **198**, 41–100.

—— KRAFT, P., MERGL, M. and MÜLLER, K. J. 1990. The problematic *Hadimopanella*, *Kaimenella*, *Milaculum* and *Utahphospha* identified as sclerites of Palaeoscolecida. *Lethaia*, **23**, 217–221.

HOU XIAN-GUANG and SUN WEI-GUO 1988. [Discovery of Chengjiang fauna at Meishucun, Jinning, Yunnan]. *Acta Palaeontologica Sinica*, **27**, 1–12, pls 1–3. [In Chinese with English summary].

—— and CHEN JUN-YUAN 1989. [Early arthropod-annelid intermediate sea animal, *Luolishania* gen. nov. from Chengjiang, Yunnan]. *Acta Palaeontologica Sinica*, **28**, 1–15, pls 1–4. [In Chinese with English summary].

HOWELL, B. F. 1962. Worms. 144–177. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part W.*